Meta-population Modeling of Narwhals, *Monodon monoceros*, in East Canada and West Greenland

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Introduction

Individual narwhals, *Monodon monoceros*, return to the same summer grounds year after year, with a meta-population structure that reflects the geographical distinctiveness of the areas (Heide-Jørgensen et al., 2013). This study identifies eight aggregations, or stocks, of narwhal in the Baffin Bay region of East Canada and West Greenland (JWG, 2015a). We examine the local dynamics of these stocks to assess the cumulated impacts of hunting in the overall area.

We perform our assessment within the Joint Working Group (JWG) of the North Atlantic Marine Mammal Commission (NAMMCO) and the Canada/Greenland Joint Commission on Conservation and Management of Narwhal and Beluga (JCNB). A main challenge is the divergence between the population structure and the geographical and yearly structure of the hunt. Hunts occur not only on summer grounds, but also on spring/fall migration and winter grounds where they target individuals from several summer aggregations (Watt and Hall, 2018; Garde and Heide-Jørgensen, 2019). This led to the development of a catch allocation model that uses satellite tracking, expert judgment, and abundance estimates to allocate the catches from 24 seasonal and geographically separated hunts among the eight summer aggregations of narwhals (JWG, 2015a; Watt et al., 2019).

We use the allocation model to estimate historical catch distributions for each of the eight summer aggregations. Population dynamic models then use these distributions to assess the impacts of the hunt. We integrate the catch allocation and population dynamics models to assess the sustainability of current and future catches, as identified by the cumulated impacts of the 24 hunts on the eight narwhal aggregations.

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Catch Allocation

The geographical locations of the eight summering areas and the different hunting grounds are shown in Watt et al. (2019: Fig. 1 and 2). The catch allocation model (Watt et al., 2019) uses an allocation matrix ($A_{i,j,t}$) to transform

$$c_{i,t} = \sum_{j=1}^{24} A_{i,j,t} H_{j,t} \qquad (1)$$

the catch histories ($H_{j,t}$) of total removals in the 24 hunts (Suppl. Tables S1 and S2) into catch histories ($c_{i,t}$) for the eight summer stocks (i:stock; j:hunt; t:year).

The allocation matrix gives the proportion of the jth hunt that is taken from the ith summer aggregation in year t, and it is estimated

$$A_{i,j,t} = \frac{P_{i,j} N_{i,t}}{\Sigma_i P_{i,j} N_{i,t}} \qquad (2)$$

from the proportional availability ($P_{i,j}$) of the individuals in the different summer aggregations to the different hunts, and the abundance of the different summer aggregations ($N_{i,t}$). This calculation assumes that for each summer aggregation there is a proportion between zero and one, $P_{i,j}$, that is available to hunters during the hunting period on the hunting grounds. All the individuals that are available to a hunt from different stocks are then at equal risk of being taken in the hunt.

Availability Matrix

The cells in the proportional availability matrix (P, Table 1) reflect the

ABSTRACT—Narwhals, Monodon monoceros*, in the Baffin Bay region of East Canada and West Greenland are aggregated into eight summer stocks, and they are hunted in 24 geographically and seasonally separated hunts. Several of the hunts target animals from different stocks, making sustainable management challenging.*

We develop a meta-population model to face the challenge. We use a catch allocation model to allocate the catches in the different hunts into historical time-series distributions for the total removals from each stock. Bayesian population dynamic modeling then analyzes the impacts of the 24 hunts on the eight stocks. The catch allocation, however, depends on the population dynamics. Thus, we integrate the allocation and population modeling in iterative runs until the estimated catch histories and population trajectories converge.

This framework is useful for sustainability assessment and management practices. The allocation model assigns catches to stocks, and the population modeling estimates sustainability for each stock. When done in retrospect it judges the sustainability of current takes. Acting on these measures, managers can use forward projections to identify overall hunting patterns that secure sustainability for all narwhals in the Baffin Bay region.

Table 1.—The proportional availability matrix (*P*) of narwhals from summer aggregations to hunting regions, as defined by beta(α,β) distributions where α = *x*+1 and β = *y*–*x*+1, with *x*/*y* being the availability ratio (*x*: available; *y*: total). Numbers O and 1 are defined zeros (*x*/*y* = 0/9999) or hunts (*x*/*y* = 9999/9999), bold numbers are partial hunts, and *x*/*y* = 0/*n* is probable zeros and *x*/*y* = *n*/*n* probable hunts for sensitivity analysis by changes in *n*. Summer aggregations: Smith: Smith Sound; Jones: Jones Sound; Inglefield: Inglefield Bredning; Melville: Melville Bay; Somerset: Somerset Island; Admirality: Admirality Inlet; Eclipse: Eclipse Sound; Baffin: East Baffin Island. Hunts: CCA: Canadian Central Arctic; BIC: Central Baffin Island; BIS: South Baffin Island.

Hunt	Season	Smith	Jones	Inglefield	Melville	Somerset	Admiralty	Eclipse	Baffin
Etah	Spring	1	0/***n***	0	0	0	0	0	0
Qaanaaq	Summer	0	0	1	0	0	0	0	0
Grise Fjord	Spring	0/***n***	1	0/***n***	0	0/***n***	0	0	0
Grise Fjord	Summer	0	1	0	0	0	0	0	0
Grise Fjord	Fall	0/***n***	1	0/***n***	0	0/***n***	0	0	0
Upernavik	Summer	0	0	0	1	0	0	0	0
Ummannaaq	Fall	0/***n***	0/***n***	0/***n***	**1/9**	1	**0/42**	**0/26**	0/***n***
Disko Bay	Winter	0/***n***	0/***n***	0/***n***	**1/7**	0/***n***	**1/42**	**1/6**	0/***n***
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/***n***	1	**6/26**	0
Pond Inlet	Spring	0	0/***n***	0/***n***	0	**2/2**	**4/4**	1	0/***n***
Pond Inlet	Summer	0	0	0	0	0	0	1	0
Pond Inlet	Fall	0	0/***n***	0/***n***	0	**0/14**	**4/42**	1	0/***n***
BIC	Spring	0	0/***n***	0/***n***	0	**0/2**	**0/4**	**0/6**	1
BIC	Summer	0	0	0	0	0	0	0	1
BIC	Fall	0	0/***n***	0/***n***	0	**0/5**	**10/42**	**16/26**	1
BIS	Spring	0	0	0	0	**0/2**	**0/4**	**0/6**	***n*/*n***
BIS	Summer	0	0	0	0	0	0	0	1
BIS	Fall	0	0	0	0	**0/5**	**0/42**	**2/26**	***n*/*n***
BIS	Winter	0	0	0	0	**0/2**	**0/42**	**1/6**	***n*/*n***

migration of narwhals in the overall region, as determined from satellite tracking and expert knowledge. The JWG (2015a) reviewed each cell in the matrix and gave it one of five designations:

Defined zero: Cells with unlikely hunts. Like hypothetical summer hunts that take animals from different areas (narwhals that are harvested by Grise Fjord during summer are from Jones Sound by definition, and they are thus not taken from the Melville Stock), and hunting areas that are not visited by a summer stock given known movements.

Probable zero: Unlikely hunts with no tracking data. The summer aggregation is unlikely hunted, but proximity and/or migration do not rule out potential takes.

Partial hunt: Satellite tracking shows that at least some of the animals in the summer aggregation are available to the hunt.

Probable hunt: Likely hunts with no tracking evidence. The summer aggregation is likely to be fully available to the hunt given geographical proximity and/or migration.

Defined hunt: Hunts on stocks in their summer area or known winter area.

Each cell in P is parameterised as a beta(α,β) distribution, where $\alpha = x + 1$ and $\beta = y - x + 1$ depends on the designation of the hunt: For a partial hunt that is parameterised by the seasonal and geographical distribution of y satellite tracked individuals, x is the number of the individuals that migrated to the hunting ground; Defined zeros are obtained by $x = 0$ and $y = 9999$; Defined hunts by $x = 9999$ and $y = 9999$; Probable zeros by $x = 0$ and $y = n$; and Probable hunts by $x = y = n$. The simulations in this paper set $n = 9999$, which implies that they do not distinguish between probable and defined designations.

Catch Histories

Watt and Hall (2018) and Garde and Heide-Jørgensen (2019) estimated catch histories of total removals for each hunt from reported catches and best knowledge on struck and loss (Table S1 and S2). The transformation of these catches by Eq. (1) into catch histories for each of the eight stocks occurs with a fixed value for each cell in the allocation matrix. Hence, to capture the uncertainty in the allocation—as represented by the uncertainty of the proportional availability matrix and the uncertainty on the abundance of the different summer aggregations—we used simulations with random draws to generate catch history distributions for all summer aggregations.

For a given year, we use an abundance estimate with a coefficient of variation (CV) for all summer aggregations. The distributions of catch histories for the summer aggregations are then generated by a large number of runs of the allocation model over the entire catch history with yearly random draws of each abundance estimate (log-normal based on point estimate and CV) and cell in the proportional availability matrix (with draws from the underlying beta distributions).

To obtain abundance estimates with CV's for all years for all summer aggregations we use subsequent runs of the catch allocation and population dynamic models. For an initial run of the allocation model, the abundance and CV estimates for a given summer aggregation are the linear time transitions between the available survey es-

Table 2.—Absolute and relative [in brackets] abundance estimates (with CV's) for the modeling of the eight summer aggregations of narwhal (from Heide-Jørgensen et al., 2010; Hansen et al.[1]; JWG, 2015a; Higdon and Ferguson, 2017; Doniol-Valcroze et al.[2]). Winter surveys from West Greenland (Heide-Jørgensen and Acquarone, 2002) and the North Water (Heide-Jørgensen et al., 2016) have uncertain stock origin and are not included in the modeling.

Year	Smith	Jones	Inglefield	Melville	Somerset	Admiralty	Eclipse	Baffin
1975	-	-	-	-	-	28260; 0.22	-	-
1981	-	-	-	-	32520; 0.1	-	-	-
1985	-	-	[3164; 0.13]	-	-	16400; 0.43	-	-
1986	-	-	8710; 0.25	-	-	-	-	-
1996	-	-	-	-	45360; 0.35	-	-	-
2001	-	-	[2297; 0.35]	-	-	-	-	-
2002	-	-	[1478; 0.25]	-	35810; 0.43	-	-	-
2003	-	-	-	-	-	5360; 0.5	-	10070; 0.31
2004	-	-	-	-	-	-	20230; 0.36	-
2007	-	-	8370; 0.25	6020; 0.86	-	-	-	-
2009	-	-	-	-	-	-	-	-
2010	-	-	-	-	-	18050; 0.22	-	-
2012	-	-	-	2980; 0.39	-	-	-	-
2013	16360; 0.65	12690; 0.33	-	-	49770; 0.2	35040; 0.42	10490; 0.24	17560; 0.35
2014	-	-	-	3090; 0.5	-	-	-	-

[1]Hansen, R. G., S. Fossette, N. H. Nielsen, M. H. S. Sinding, D. Borchers, and M. P. Heide-Jørgensen. 2015. Abundance of narwhals in Melville Bay in 2012 and 2014. NAMMCO/SC/22-JCNB/SWG/2015-JWG/14.

[2]Doniol-Valcroze, T., J. F. Gosselin, D. Pike, J. Lawson, N. Asselin, K. Hedges, and S. Ferguson. 2015. Abundance estimates of narwhal stocks in the Canadian High Arctic in 2013. DFO. Can. Sci. Advis. Sec. Res. Doc. 2015, 60 p. (Avail. at https://waves-vagues.dfo-mpo.gc.ca/Library/362110.pdf).

timates in Table 2. The abundance in subsequent runs are instead the trajectories that were estimated by the previous run of the population dynamic models, given the catch histories that were estimated by the previous run of the allocation model. This iterative running of the two models occurs until convergence of the catch histories and abundance trajectories.

Population Dynamics

Separate population models with density regulated growth were constructed for each of the eight summer aggregations of narwhals. All the models were based on an age and sex structured Bayesian modeling framework that has been used in earlier applications for walrus, *Odobenus rosmarus* (Witting and Born, 2005, 2014), large cetaceans (Witting, 2013), beluga, *Delphinopterus leucas* (Heide-Jørgensen et al., 2016a,b), and narwhal (e.g., Witting and Heide-Jørgensen[1,2,3]).

Some of the summer aggregations have only been surveyed once, and a full age-structured model is clearly over parameterized for these cases if the main purpose is parameter estimation by maximum likelihood. Yet, our main purpose is to use a Bayesian framework to integrate prior knowledge on the life history biology of narwhals with survey estimates of abundance for the construction of realistic population dynamic models.

Witting[4] used the case of belugas in West Greenland to analyze for influence of model uncertainty in the construction of realistic population models in Bayesian assessments of density regulated growth. Assessments were made for one age-structured and four structurally different discrete models, with all assessments being based on the same data. All models gave very similar estimates of current abundance and current production levels.

We chose an age and sex structured framework that allows the model to be constructed directly from our prior knowledge of the life history of narwhals. This allows also for a later inclusion of sex structured catches and age-structured catch data, as done in other assessments (Hobbs et al., 2015; Witting and Heide-Jørgensen[1,2,3]). Age-structured data, however, were not included here, as we wanted to keep the population dynamic models relatively simple, comparable across summer aggregations, and fast to simulate.

Let $A = 15$ be the maximum lumped age-class of the model. Let the number $N^{m/f}_{a,t+1}$ of males (m) and females (f) in age-classes $0 < a < A$ in year $t + 1$ be

$$N^{m/f}_{a+1,t+1} = p^{m/f}_a N^{m/f}_{a,t} - c^{m/f}_{a,t} \quad (3)$$

and the number of animals in age-class A be

$$N^{m/f}_{A,t+1} = p^{m/f}_A N^{m/f}_{A,t} + p^{m/f}_{A-1} N^{m/f}_{A-1,t} - c^{m/f}_{A,t} - c^{m/f}_{A-1,t} \quad (4)$$

where $p^{m/f}_a$ is the age specific survival rate of males/females, and $c^{m/f}_{a,t}$ is the age specific catch of males/females in year t. The age and gender (g) dependent survival rates $p^g_a = p\tilde{p}^g_a$ are given as a product between a survival scalar p and a relative ($0 < \tilde{p}^g_a \leq 1$) survival rate, with relative survival being one for males and females older than one year of age. The age and gender specific catches $c^{m/f}_{a,t} = c^{m/f}_t \tilde{c}^{m/f}_a$ in year t is given as a product between the total catch of males/females ($c^{m/f}_t$), as specified by the catch history, and an age-specific catch selectivity ($\tilde{c}^{m/f}_t$) that is uniform except that no animals are taken from age-class zero.

The number of females and males in age-class zero is $N^f_{0,t} = \vartheta N_{0,t}$ and $N^m_{0,t} = (1-\vartheta)N_{0,t}$, where ϑ is the fraction of females at birth, and

$$N_{0,t} = \sum_{a=a_m}^{A} B_{a,t} \quad (5)$$

where a_m is the age of the first reproductive event and $B_{a,t}$, the number of births from females in age-class a, is

$$B_{a,t} = b_{a,t}\tilde{b}_a M^f_{a,t} \quad (6)$$

where $b_{a,t}$ is the birth rate in year t for age-class a females should they be at their age-specific reproductive peak, $0 < \tilde{b}_a \leq 1$ is the relative age-specific birth rate (1 for all mature females), and $M^f_{a,t}$ is the number of mature females in age-class a in year t, defined as

$$M^f_{a,t} = \begin{cases} 0 & \text{if } a < a_m \\ N^f_{a,t} & \text{if } a \geq a_m \end{cases} \quad (7)$$

Let $b_{a,t}$ be

[1]Witting, L., and M. P. Heide-Jørgensen. 2012a. Assessment of East Greenland narwhals. NAMMCO/SC/19-JCNB/SWG/2012-JWG/12.

[2]Witting, L., and M. P. Heide-Jørgensen. 2012b. Assessment of West Greenland narwhal (excluding Uummannaq). NAMMCO/SC/19-JCNB/SWG/2012-JWG/10.

[3]Witting, L., and M. P. Heide-Jørgensen. 2012c. Estimation of dynamics for narwhals in Uummannaq, West Greenland. NAMMCO/SC/19-JCNB/SWG/2012-JWG/11.

[4]Witting, L. 2009. Model uncertainty on assessments of West Greenland beluga and narwhals. NAMMCO/SC/16-JCNB/SWG/2009-JWG/12.

$$b_{a,t} = b^* + [b_{\max} - b^*][1 - (\hat{N}_t/\hat{N}^*)\gamma] \quad (8)$$

for density regulated growth where b^* is the birth rate at population dynamic equilibrium (assuming zero catch and equilibrium denoted by $*$), b_{max} is the maximal birth rate, γ is the density dependence parameter, and the abundance component that imposes density dependence is the one-plus component

$$\hat{N}_t = \sum_{a=1}^{A} N^f_{a,t} + N^m_{a,t} \quad (9)$$

Given a stable age-structure and no catch, let λ be a constant defined by $\hat{N}_{t+1} = \lambda \hat{N}_t$. The sustainable yield is then $sy = \hat{N}(\lambda - 1)$, with an optimum $\partial sy/\partial \hat{N} = 0$; the maximum sustainable yield (msy) at $\hat{N}_{msy}$, also known by the maximum sustainable yield rate (msyr = $msy/\hat{N}_{msy}$) and the maximum sustainable yield level (msyl = $\hat{N}_{msy}/\hat{N}^*$).

Statistical Methods

The population dynamic model for each summer aggregation was fitted to the abundance estimates for that stock (Table 2) by subtracting the historical catches from the projection. The eight narwhal stock models provide an interlinked meta-population model by the allocation of catches from the 24 hunts. When catches have been allocated among the different stocks, the fitting of each of the eight population dynamic models occurs independently of the seven other models. The only statistical link between the eight models is the dependence of the catch allocation on the simulated abundance trajectories, and this calculation occurs in-between the independent fits where the population models use the catch histories from the previous run of the allocation model.

One implication of this statistical independence of the eight population dynamic models is that the meta-population model is robust to unbalanced data sets. Should there be more abundance data for one stock compared with others, and/or should age-structured data be included only for some stocks, the likelihood of the data-rich stocks would not dominate an overall likelihood with the risk of biasing the parameter estimates for the data-poor stocks.

The independent estimation of each of the eight population models is done using the same Bayesian statistical method (e.g., Berger, 1985; Press, 1989), where posterior estimates of model parameters and other management related outputs are calculated. This implies an integration of the product between a prior distribution for each parameter and a likelihood function that links the probability of the data to the different parameterizations of the model.

Table 3.—Prior distributions for the different models (*M*). The list of parameters: N_0 is the initial abundance, N^* the population dynamic equilibrium abundance, 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 the bias of the relative abundance estimate for Inglefield Bredning. Abundance is given in thousands. The prior probability distribution is given by superscripts; *u*: uniform (min,max), *U*: log uniform (min,max), *b*: beta $\left\{ {}^{a,b}_{i,x} \right\}$ with *i*=min and *x*=max, and *f*: file distribution. No superscript: fixed value.

M	N_0	N^*	p	P_0	b	a_m	ϑ	γ	C_h	β
Smith	-	$2{,}80^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-
Jones	-	$2{,}60^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-
Inglefield	$1{,}25^U$	$3{,}30^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	$0.01{,}1^U$
Melville	$0.8{,}20^U$	$3{,}30^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-
Somerset	$5{,}60^U$	$25{,}90^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-
Admiralty	-	$10{,}40^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-
Eclipse	-	$5{,}50^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-
Baffin	-	$3{,}60^U$	2.2^b 0.95,1	$0.5{,}1^u$	0.33	2.2^b 7,15	0.5	$2{,}4^u$	f	-

Prior Distributions

Each of the eight population models start in 1970 with the same priors on the biological parameters (see Table 3). Earlier applications for narwhals have used uniform priors for adult survival (p) and the age of first reproduction (a_m). Following discussions at JWG (2018), these were changed to symmetric hump-formed beta distributions ($a = b = 2$) that allocate more weight on the center of the distributions. Given our best knowledge on narwhal life histories (Garde and Heide-Jørgensen[5]), the assumed minimum and maximum values were set to 0.95 and 0.995 for p, and 7 and 15 years for a_m.

As the birth rate (b) and first year survival (p_0) multiply together to determine the number of narwhal at age one, we decided to set the prior on b to a single value, instead of a distribution, in order to reduce the number of parameter estimates. This value was set to 0.33 to reflect the widespread 3-year calving interval in narwhals. As for many other species, there is hardly any knowledge on first year survival in narwhal, except that it is likely to be smaller and more fluctuating than adult survival. We use a uniform prior from 0.5 to 1 for p_0, to capture a first year survival that range from $p/2$ to p.

Admiralty Inlet and all the summer aggregations with only one or two abundance estimates available (Smith Sound, Jones Sound, Eclipse Sound, East Baffin Island) seems to have had a very low exploitation rate in the beginning of the period. For these we assumed that the population was close to carrying capacity in 1970. For the remaining aggregations (Inglefield Bredning, Melville Bay, Somerset Island), with a somewhat larger historical exploitation, we assume that the abundance in 1970 was smaller than carrying capacity. Hence, for each prior draw of the carrying capacity, we continued to draw the 1970 abun-

[5]Garde, E., and M. P. Heide-Jørgensen. 2017. Update on life history parameters of narwhals (*Monodon monoceros*) from East and West Greenland. North Atlantic Marine Mammal Commission/Joint Commission on Narwhal and Beluga Report NAMMCO/SC/24-JCNB/SWG/2017-JWG/16.

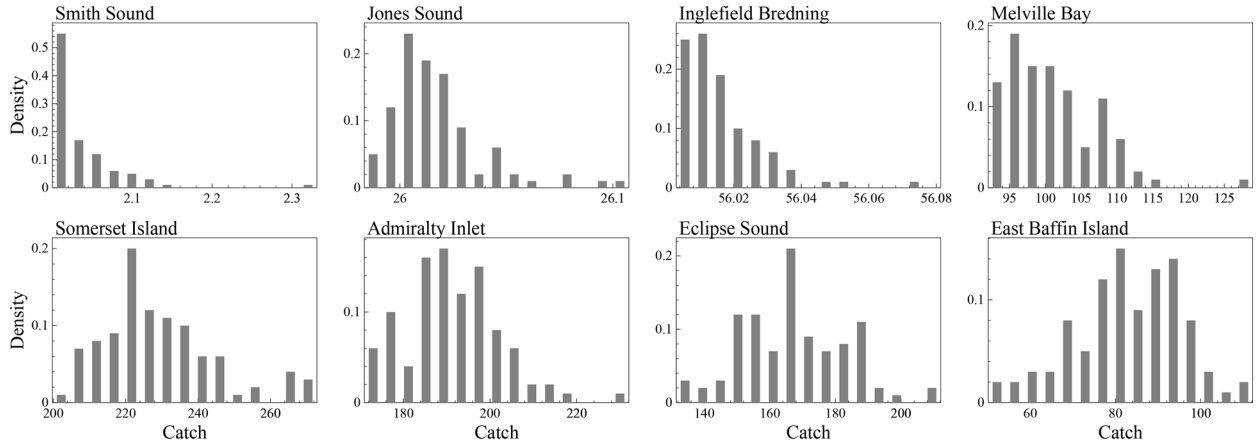

Figure 1.—Catch distributions per summer aggregation, estimates for year 2011.

dance from the prior until the latter was smaller than the former.

The allocation model estimated the catch distributions over the complete catch history starting in 1970. We used these distributions to generate catch priors for the population models, with draws from the prior generating specific catch histories for each iteration of a population model.

The prior distributions of catches for a given year were based on distributions of total removals that were estimated for 2011 by 200 random draws of the allocation model (Fig. 1). The choice of 2011, instead of another year, is rather arbitrary, except that we wanted to use a relatively recent year with high confidence in the reporting of catches. The prior distributions of the catches in time were based on two complete catch histories, a minimum catch history (c_{min}, set to the 1th percentile of the distribution of catches for given years) and a maximum catch history (c_{max}, 99th percentile). The 2011 distribution was then rescaled to run from zero to one, with a value (x) drawn at random from this distribution for each parameterization of a population model, with the catch history for the iteration being calculated as $c_t = c_{min,t} + x(c_{max,t} - c_{min,t})$.

Bayesian Integration

The Bayesian integration was obtained by the sampling-importance-resampling routine (Jeffreys, 1961; Berger, 1985; Rubin, 1988), where n_s random parameterizations θ_i ($1 \le i \le n_s$) are sampled from an importance function $h(\theta)$. This function is a probability distribution function from which a large number, n_s, of independent and identically distributed draws of θ can be taken. $h(\theta)$ shall generally be as close as possible to the posterior, however, the tails of $h(\theta)$ must be no thinner (less dense) than the tails of the posterior (Oh and Berger, 1992). For each drawn parameter set θ_i the population was projected from the first year with a harvest estimate to the present. For each draw an importance weight, or ratio, was calculated

$$w(\theta_i) = \frac{L(\theta_i)\,p(\theta_i)}{h(\theta_i)} \qquad (10)$$

where $L(\theta_i)$ is the likelihood given the data, and $h(\theta_i)$ and $p(\theta_i)$ are the importance and prior functions evaluated at θ_i. In the present study the importance function is set to the joint prior, so that the importance weight is given simply by the likelihood. The n_s parameter sets were then re-sampled n_r times with replacement, with the sampling probability of the ith parameter set being

$$q_i = \frac{w(\theta_i)}{\sum_{j=1}^{n_s} w(\theta_j)} \qquad (11)$$

This generates a random sample of the posterior distribution of size n_r.

The likelihood L was calculated under the assumption that observation errors are log-normally distributed

$$L = \prod_i \prod_t \exp\left(-\frac{[\ln(\hat{N}_{i,t}/\beta_i N_t)]^2}{2cv_{i,t}^2}\right)/CV_{i,t} \qquad (12)$$

where $\hat{N}_{i,t}$ is the point estimate of the ith set of abundance data in year t, $CV_{i,t}$ is the coefficient of variation of the estimate, N_t is the simulated abundance, and β_i a bias term which is set to one for absolute abundance estimates.

Management Objectives

We use the Bayesian framework to estimate the probabilities of meeting an assumed management objective for potential future catches from each of the eight narwhal populations. We usually calculate our advice for the JWG by projecting five years into the future, with an assessment in year t calculating sustainability over the period from t to $t + 5$.

Given future annual catches c in the period t to $t + 5$, we apply the objective

$$\text{ob} = \begin{cases} N_{t+5} > N_t & \text{if } N_t < N^* \text{msyl} \\ c \le 0.9\ \text{msy} & \text{if } N_t \ge N^* \text{msyl} \end{cases} \qquad (13)$$

Given the population dynamic model and the data, the probability of meeting the objective (ob) is straightforwardly calculated from the Bayesian

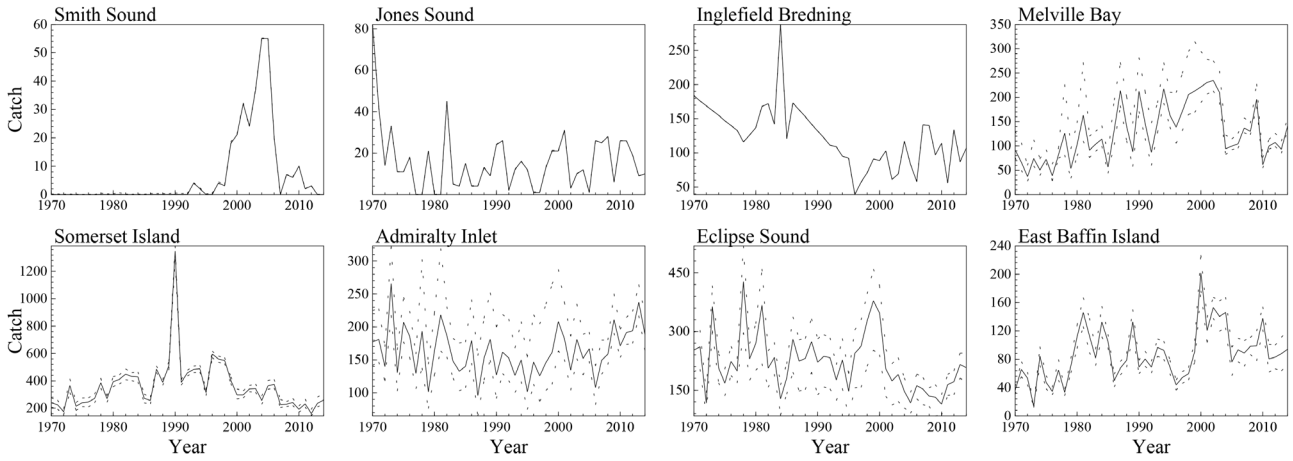

Figure 2.—Yearly catches per summer aggregation with 90% confidence intervals.

statistical method. For each parameterization θ_i of the random sample of the posterior distribution of size n_r, we have perfect knowledge of the status of the population so that it can be determined whether Eq. (13) is true or false. Hence, the probability $p(\text{ob})$ of meeting the objective is

$$p(ob) = \sum_{i=1}^{n_r} g(\theta_i, c)/n_r$$
$$g(\theta_i, c) = \begin{cases} 1 & \text{if ob is true} \\ 0 & \text{if ob is false} \end{cases} \quad (14)$$

with the sum given over the complete random sample of the posterior distribution.

The sustainability of the hunts operates at the population level, but our recommendations on future use relate to hunting grounds. To achieve this, for a given set of potential future catches across hunts, we use the allocation model to calculate the distributions of future catches for the eight populations, with these distributions reflecting the uncertainty in the allocation of catches between populations. We can then calculate the probability of meeting the management objective for each percentile of the catch distribution for each population. This allows for an adjustment of the potential catches in future hunts until the probabilities of fulfilling management objectives exceed agreed thresholds for all populations.

Results and Discussion

The catch distributions and abundance trajectories of the allocation and population dynamic models need relatively few iterative simulations to converge, with stable estimates obtained after four to five iterations (Suppl. Fig. 1).

The estimated catch distributions (Fig. 2) are extremely narrow for Smith Sound, Jones Sound, and Inglefield Bredning. As evident from the proportional availability matrix (Table 1), this reflects a migration and hunting pattern where these animals are taken almost exclusively on their summer grounds. The catch history for Sommerset Island has a slightly wider distribution that reflects animals taken in combinations with animals from other summer grounds during the fall hunt in Ummannaaq and the spring hunt in Pond Inlet. Being harvested in several multi-stock areas during winter and migration, the catch distributions for Melville Bay, Admirality Inlet, and Eclipse Sound are wider.

The sampling statistics of the last run of the Bayesian population models (Suppl. Table S3) indicate no problems with conversion, as evident also from the posterior and realised prior distributions for all parameters across all models (Suppl. Fig. S2–S9). The posterior updating of the population models fall in two groups, as illustrated by the selected distributions for Jones Sound and Inglefield Bredning in Figure 3. The abundance data for most populations except Inglefield Bredning, Somerset Island, and Admirality Inlet are too few to update the priors on the life history and growth rate related parameters. As illustrated by Jones Sound, this implies posterior estimates that resemble the priors for all parameters, except abundance that is strongly updated for all models. For Inglefield Bredning there is also an updating of the life history parameters, which reflects abundance and catch data that indicate a somewhat smaller growth rate than expected by the prior.

The lack of updating shows that most of the posterior estimates in Table 4 should not be regarded as parameter estimates that follow from the abundance and catch data, but more like best estimates for narwhals in general. This raises the question of overparameterised models. Yet, the estimation of parameters is not the purpose of this study. It is instead to project narwhal populations under the constraints of not only the available abundance and catch data, but also our current knowledge on the life history of narwhals. For this to be possible, it is essential to constrain the models by priors to avoid unrealistic scenarios, and we use the best estimated life history parameters to impose these bounds.

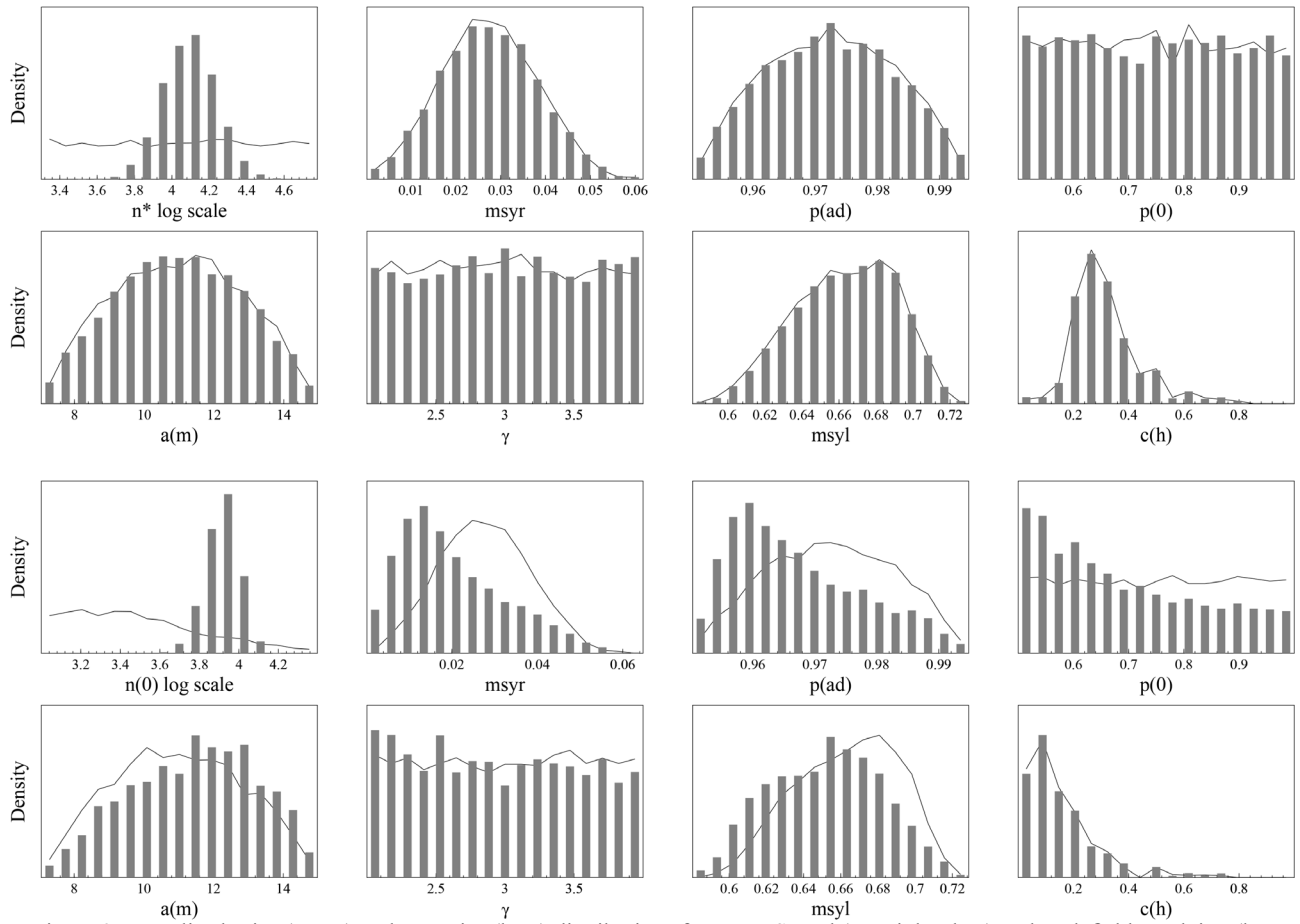

Figure 3.—Realised prior (curve) and posterior (bars) distributions for Jones Sound (top eight plots) and Inglefield Bredning (bottom plots).

Table 4.—Parameter estimates for the different models (*M*). Estimates are given by the median ($x_{0.5}$) and the 90% confidence interval ($x_{0.05}$ - $x_{0.95}$) of the posterior distributions. Abundance is given in thousands. $d = N_{2016}/N^*$.

M		N_0	N^*	*r*	msyr	*p*	p_0	a_m	γ	msyl	c_h	*d*
Smith	$x_{0.5}$	-	16	0.035	0.028	0.97	0.75	11	3	0.67	0.05	1.0
	$x_{0.05}$	-	5.5	0.013	0.01	0.96	0.53	8.1	2.1	0.62	0.006	0.98
	$x_{0.95}$	-	45	0.058	0.045	0.99	0.97	14	3.9	0.7	0.29	1.0
Jones	$x_{0.5}$	-	12	0.035	0.027	0.97	0.75	11	3	0.67	0.29	0.99
	$x_{0.05}$	-	7.2	0.013	0.0097	0.96	0.52	8.1	2.1	0.62	0.17	0.97
	$x_{0.95}$	-	21	0.058	0.046	0.99	0.97	14	3.9	0.7	0.6	1.0
Inglefield	$x_{0.5}$	8.3	11	0.023	0.018	0.97	0.66	12	2.9	0.65	0.12	0.70
	$x_{0.05}$	5.9	7.9	0.006	0.004	0.95	0.51	8.3	2.1	0.6	0.033	0.25
	$x_{0.95}$	11	25	0.056	0.044	0.99	0.95	14	3.9	0.7	0.48	0.95
Melville	$x_{0.5}$	3.8	7.6	0.037	0.029	0.97	0.77	11	3	0.67	0.16	0.39
	$x_{0.05}$	2	4.4	0.015	0.012	0.96	0.53	8	2.1	0.62	0.026	0.11
	$x_{0.95}$	6.8	25	0.06	0.047	0.99	0.98	14	3.9	0.71	0.49	0.78
Somerset	$x_{0.5}$	23	51	0.038	0.029	0.97	0.77	11	3	0.67	0.36	0.92
	$x_{0.05}$	17	36	0.022	0.017	0.96	0.54	8	2.1	0.62	0.075	0.59
	$x_{0.95}$	32	83	0.058	0.045	0.99	0.98	14	3.9	0.71	0.82	0.98
Admiralty	$x_{0.5}$	-	21	0.035	0.027	0.97	0.74	11	3	0.66	0.37	0.92
	$x_{0.05}$	-	17	0.012	0.009	0.96	0.52	8	2.1	0.61	0.086	0.80
	$x_{0.95}$	-	26	0.057	0.045	0.99	0.97	14	3.9	0.7	0.7	0.96
Eclipse	$x_{0.5}$	-	15	0.036	0.028	0.97	0.76	11	3	0.67	0.38	0.87
	$x_{0.05}$	-	11	0.013	0.01	0.96	0.53	8	2.1	0.62	0.077	0.63
	$x_{0.95}$	-	20	0.06	0.046	0.99	0.98	14	3.9	0.71	0.75	0.96
Baffin	$x_{0.5}$	-	13	0.036	0.028	0.97	0.76	11	3	0.67	0.52	0.94
	$x_{0.05}$	-	9.2	0.015	0.011	0.96	0.53	8	2.1	0.62	0.2	0.83
	$x_{0.95}$	-	19	0.058	0.045	0.99	0.98	14	3.9	0.7	0.77	0.98

The estimated population trajectories and underlying abundance data illustrate the general absence of evidence for trends in the available data, with the only exception being perhaps Somerset Island (Fig. 4). We note that the relative data-rich trajectory for Inglefield Bredning is flat, despite the somewhat lower growth rate estimate relative to the other summer aggregations.

Having realistic models for the eight stocks given the data, we estimate future sustainability by projecting five years into the future. From the last assessment of the JWG (2015b), we show the estimated trade-off between the future catch and the probability of fulfilling the management objective for all stocks in Supplementary Table S4. The size of the sustainable

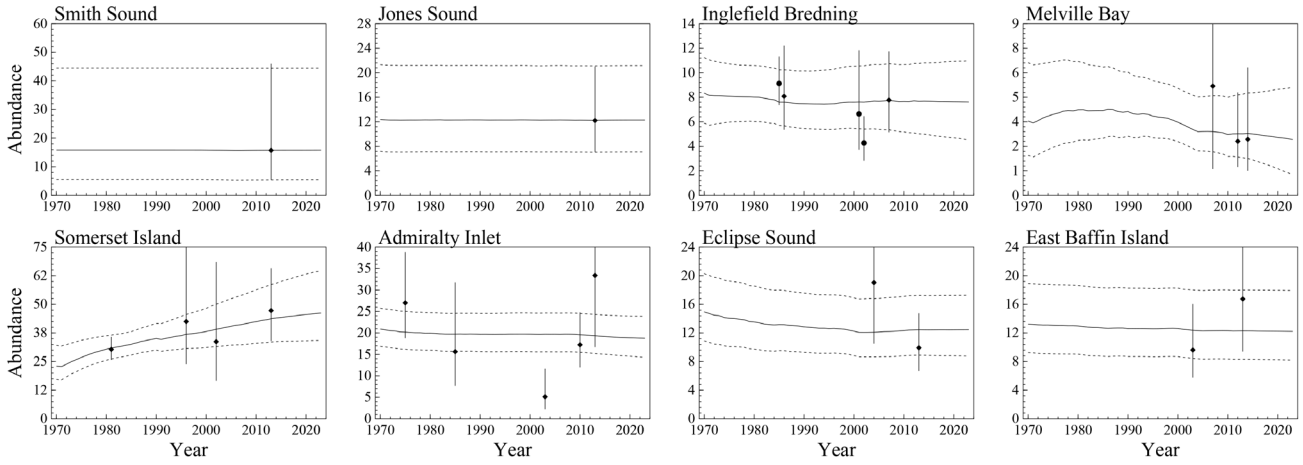

Figure 4.—Trajectories of the different narwhal aggregations. Points with bars are the abundance estimates with 90% confidence intervals. Solid curves are the median, and dotted curves mark the 90% confidence interval, of the estimated models. Abundance is given in thousands.

Table 5.—Examples (C#) of future annual removals per hunting region.

Hunt	Season	C0	C1
Etah	Spring	4	5
Qaanaaq	Summer	98	98
Grise Fjord	Spring	7	9
Grise Fjord	Summer	11	15
Grise Fjord	Fall	0	0
Upernavik	Summer	100	70
Ummannaaq	Fall	86	154
Disko Bay	Winter	73	97
CCA	Spring	4	6
CCA	Summer	74	118
CCA	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
BIC	Spring	12	11
BIC	Summer	100	91
BIC	Fall	44	40
BIS	Spring	5	5
BIS	Summer	9	8
BIS	Fall	12	11
BIS	Winter	0	0

Table 6.—Examples of future annual removals (C#) per summer aggregation, with associated probabilities (P#) of fulfilling management objectives for the eight stocks. The different removals follow from the catch options in Table 5, and the 90% confidence intervals of the estimates are given by sub- and superscripts.

Item	Smith	Jones	Inglefield	Melville	Somerset	Admiralty	Eclipse	Baffin
C0	4_{4}^{4}	18_{18}^{18}	98_{98}^{98}	109_{141}^{141}	219_{175}^{265}	185_{161}^{226}	155_{104}^{207}	134_{120}^{152}
P0	$1.00_{1.00}^{1.00}$	$1.00_{1.00}^{1.00}$	$0.70_{0.70}^{0.70}$	$0.49_{0.26}^{0.56}$	$0.99_{0.99}^{0.99}$	$0.89_{0.83}^{0.92}$	$0.95_{0.89}^{0.98}$	$0.76_{0.68}^{0.81}$
C1	5_{5}^{5}	24_{24}^{24}	98_{98}^{98}	83_{72}^{126}	343_{283}^{399}	243_{212}^{296}	198_{134}^{262}	122_{110}^{138}
P1	$1.00_{1.00}^{1.00}$	$1.00_{1.00}^{1.00}$	$0.70_{0.70}^{0.70}$	$0.70_{0.36}^{0.75}$	$0.97_{0.95}^{0.98}$	$0.80_{0.71}^{0.85}$	$0.90_{0.80}^{0.96}$	$0.80_{0.74}^{0.85}$

catch reflects the size of the stocks. With a 2014 estimate of 3,090 (cv:0.5) animals, Melville Bay is the smallest summer aggregation and no more than 63 individuals should be taken annually from this stock if we want the objective secured with 80% probability. With a 2013 estimate of 49,770 (CV:0.2) narwhals, the largest aggregation occurs around Sommerset Island, and this stock may take an annual removal around 635 individuals given sustainability with 80% probability.

It is, however, impossible to impose regulating quotas directly on narwhal stocks because the hunt occurs not only on summer grounds but also in mixed winter, spring and fall areas. Regulation may instead occur on the different hunts, with Table 5 showing two potential takes that were considered at JWG (2015b). The first (C0) is the average take over the 5-year period from 2009 to 2013, and the second (C1) a more sustainable alternative. These takes are calculated into sustainability measures for the eight stocks in Table 6. It gives the probability of meeting the management objective for the eight stocks, given annual takes of C0 or C1. These probabilities have 90% confidence intervals (CI) that reflect the uncertainty on the origin of the animals that are taken in the different hunts.

Our chances of fulfilling the objective is high for most stocks if the catches from 2009 to 2013 (C0) are continued until 2020. The chances, however, would be no more than 49% (90% CI:26%–56%) for Melville Bay and 76% (90% CI:68%–81%) for East Baffin Island. The C1 option takes 195 narwhals more per year than the C0 option, yet, at the median level, the C1 option ensures a 70% chance of meeting the objective for the two stocks that summer in Greenland (Inglefield Bredning and Melville Bay), and at least a 80% chance for the remaining stocks in Canada. A redistribution of the catches may thus allow for a higher harvest that ensures also a higher minimum level of sustainability across all stocks.

This example illustrates how the meta-population modeling of narwhals in East Canada and West Greenland is a useful tool for sustainability assessment and management practice. The catch allocation model solves the problem of assigning catches to stocks, and the population dynamic modeling takes these catch distributions and calculates sustainability for each of the

eight narwhal stocks. When done retrospectively it judges the sustainability of current takes. Acting on these measures, managers may change the current takes on the 24 hunting grounds and identify hunting patterns that are sustainable for all narwhals in the Baffin Bay region.

Literature Cited

Berger, J. O. 1985. Statistical decision theory and Bayesian analysis. Second ed. SpringerVerlag, N.Y., 617 p.

Garde, E., R. H. Hansen, and M. P. Heide-Jørgensen. 2019. Narwhal, *Monodon monoceros*, catch statistics in Greenland, 1862–2017. Mar. Fish. Rev. 81(3–4):105–115 (doi: https://doi.org/10.7755/MFR.81.3-4.6).

Heide-Jørgensen, M. P., and M. Acquarone. 2002. Size and trends of the bowhead whale, beluga and narwhal stocks wintering off West Greenland. NAMMCO Sci. Pub. 4:191–210 (doi: https://doi.org/10.7557/3.2844).

_____, K. L. Laidre, M. L. Burt, D. L. Borchers, T. A. Marques, R. G. Hansen, M. Rasmussen, and S. Fossette. 2010. Abundance of narwhals (*Monodon monoceros*) on the hunting grounds in Greenland. J. Mamm. 91:1,135–1,151 (doi: https://doi.org/10.1644/09-MAMM-A-198.1).

_____, P. R. Richard, R. Dietz, and K. L. Laidre. 2013. A metapopulation model for Canadian and West Greenland narwhals. Anim. Cons. 16:331–343 (doi: https://doi.org/10.1111/acv.12000).

_____, R. G. Hansen, S. Fossette, N. H. Nielsen, D. L. Borchers, H. Stern, and L. Witting. 2016a. Rebuilding beluga stocks in West Greenland. Anim. Cons. 20:282–293 (doi: https://doi.org/10.1111/acv.12315).

_____, M. S. Sinding, N. H. Nielsen, A. Rosing-Asvid, and R. G. Hansen. 2016b. Large numbers of marine mammals winter in the North Water polynya. Pol. Biol. 39:1–10 (doi: https://doi.org/10.1007/s00300-015-1885-7).

Higdon, J. W., and S. H. Ferguson. 2017. Database of aerial surveys and abundance estimates for beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the Canadian Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 3211, 45 p. (avail. at https://waves-vagues.dfo-mpo.gc.ca/Library/4058544x.pdf).

Hobbs, R. C., P. R. Wade, and K. E. W. Shelden. 2015. Viability of a small, geographically isolated population of beluga whales, *Delphinapterus leucas*: effects of hunting, predation, and mortality events in Cook Inlet, Alaska. Mar. Fish. Rev. 77(2):59–88 (doi: https://doi.org/10.7755/MFR.77.2.4).

Jeffreys, H. 1961. Theory of probability. 3rd. Clarendon Press, Oxford, 447 p.

JWG. 2015a. Joint meeting of the narwhal catch allocation sub-group (JWGsub) of the NAMMCO scientific committee working group on the population status of the narwhal and beluga in the North Atlantic and the Canada/Greenland joint commission on conservation and management of narwhal and beluga scientific working group. NAMMCO Annu. Rep. 2015, Annex 1:281–304 (avail. at https://nammco.no/wp-content/uploads/2017/08/annual-report-2015.pdf).

_____. 2015b. Report of the meeting of the NAMMCO/JCNB, NAMMCO scientific committee working group on the population status of the narwhal and beluga in the North Atlantic and the Canada/Greenland joint commission on conservation and management of narwhal and beluga scientific working group. NAMMCO Annu. Rep. 2015, Annex 2:248–273 (avail. at https://nammco.no/wp-content/uploads/2017/08/annual-report-2015.pdf).

_____. 2018. Report of the NAMMCO-JCNB Joint Scientific Working Group on Narwhal and Beluga, 8–11 March 2017, Copenhagen, Denmark. NAMMCO Annual Report 2018, 56 p. (avail. at http://nammco.wpengine.com/wp-content/uploads/2017/06/nammco-jcnb-jwg-report-march-2017-final-with-ex-summ.pdf).

Oh, M. S., and J. O. Berger. 1992. Adaptive importance sampling in Monte Carlo integration. J. Stat. Comp. Sim. 41:143–168 (doi: https://doi.org/10.1080/00949659208810398).

Press, S. J. 1989. Bayesian statistics: principles, models, and applications. John Wiley, N.Y., 256 p.

Rubin, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. *In* J. M. Bernardo, M. H. DeGroot, D. V. Lindley, and A. M. Smith (Editors), Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, 1–5 June 1987, p. 395–402. Clarendon Press, Oxford.

Watt, C., and P. Hall. 2018. Catch statistics for narwhal (*Monodon monoceros*) in Canada from 1970–2015. Can. Tech. Rep. Fish. Aquat. Sci. 3270, 209 p. (avail. at https://waves-vagues.dfo-mpo.gc.ca/Library/40708238.pdf).

Watt, C. A., T. Doniol-Valcroze, L. Witting, R. C. Hobbs, R. G. Hansen, D. S. Lee, M. Marcoux, V. Lesage, E. Garde, S. H. Ferguson, and M. P. Heide-Jørgensen. 2019. Hunt allocation modeling for migrating animals: the case of Baffin Bay narwhal, *Monodon monoceros*. Mar. Fish. Rev. 81(3–4):125–136 (doi: https://doi.org/10.7755/MFR.81.3-4.8).

Witting, L. 2013. Selection-delayed population dynamics in baleen whales and beyond. Pop. Ecol. 55:377–401 (doi: https://doi.org/10.1007/s10144-013-0370-9).

_____ and E. W. Born. 2005. An assessment of Greenland walrus populations. ICES J. Marine Sci.62:266–284 (doi: https://doi.org/10.1016/j.icesjms.2004.11.001).

_____ and _____. 2014. Population dynamics of walruses in Greenland. NAMMCO Sci. Publ. 9:191–218 (doi: https://doi.org/10.7557/3.2612).