Hunt Allocation Modeling for Migrating Animals: The Case of Baffin Bay Narwhal, *Monodon monoceros*

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ABSTRACT— Hunted animals are often managed as static management units, or stocks, specific to hunting regions. However, movement of animals between regions poses a particular challenge for management to ensure that the hunt of individual stocks is sustainable. The incorporation of genetic information in stock assessments can improve management decisions, but the resolution of genetics may not differentiate stocks, making the use of movement data necessary. The Joint Working Group of the North Atlantic Marine Mammal Commission (NAMMCO) and the Canada-Greenland Joint Commission on Conservation and Management of Narwhal and Beluga (JCNB) has developed a model that allocates catches in different hunting regions and seasons to different stocks based on movement data, local knowledge, and expert opinion. The model uses information on stock size, catches in different hunting areas/seasons, and a matrix which estimates the proportion of animals in each stock that are available to hunters in different regions and seasons. This matrix can be informed by quantitative data on stock structure (e.g., genetics, telemetry) or qualitative information (local knowledge, expert opinion, etc.). Uncertainty in the availability of animals and individual stock sizes is incorporated in a stochastic version. The model is presented using a case study of narwhals, which are managed as stocks based on their summer distribution in Canada and Greenland.

Introduction

Marine mammal populations or stocks often have large spatial distributions and follow seasonal migration patterns that expose them to taking by hunters or other risks at different times and locations throughout the year (Heide-Jørgensen et al., 2003; Valenzuela et al., 2009; Foote et al., 2010; Horton et al., 2017), and often across many international jurisdictions (Harrison et al., 2018). Migration patterns follow predictable routes and seasonal timing such that the exposure to potential interactions with anthropogenic activities may occur at a number of locations annually each for a short period of time (Rosenbaum et al., 2013; O'Corry-Crowe et al., 2016; Forney et al., 2017; Watt et al., 2017). Understanding migration of animals and residency time becomes particularly important for sustainable management of hunted species (Harrison et al., 2018). Movement of animals has been considered particularly important for developing and implementing conservation measures (Cooke, 2008; McGowan et al., 2017), but there are few examples where movement and harvest data have been integrated for sustainable management of hunted species (although see Nichols et al., 1995).

Sustainable management of hunting typically divides species into management units, or stocks (hereafter referred to as stocks) that are thought to be self-sustaining, and often defined based on genetic indicators, residency time, site-fidelity, or other life history characteristics (Begg et al., 1999; Hobbs et al., 2019). Movement of animals among hunting regions and hunting regions in which hunters have access to more than one stock pose a particular challenge for ensuring individual stocks are managed sustainably (Allen and Singh, 2016); thus, a modeling approach that accounts for this movement and mixing of stocks is needed (Ogburn et al., 2017). In this way, removals can be attributed to the stock of origin, regardless of the time of year or location of the hunt.

In many cases, genetic samples and phenology of catches are used to estimate the portion of each stock available to hunters at different hunting sites, across seasons (de March and Postma, 2003; Shafer et al., 2014; Doniol-Valcroze et al.[1]). However, in cases such as narwhals, *Monodon monoceros*, where genetic variation is very low (Palsbøll et al., 1997; Westbury et al., 2019; Louis et al., 2020; Petersen et al.[2]) other methods such as telemetry, diet, behavioral studies, or local knowledge may be used to as-

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[1] Doniol-Valcroze, T., J.-F. Gosselin, and M. O. Hammill. 2012. Population modeling and harvest advice under the precautionary approach for eastern Hudson Bay beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2012/168:iii + 31 p. (http://waves-vagues.dfo-mpo.gc.ca/).

[2] Petersen, S. D., D. Tenkula, and S. H. Ferguson. 2011. Population genetic structure of narwhal (*Monodon monoceros*). DFO Can. Sci. Advis. Sec. Res. Doc. 2011/021:vi + 20 p. (https://waves-vagues.dfo-mpo.gc.ca/Library/343698.pdf).

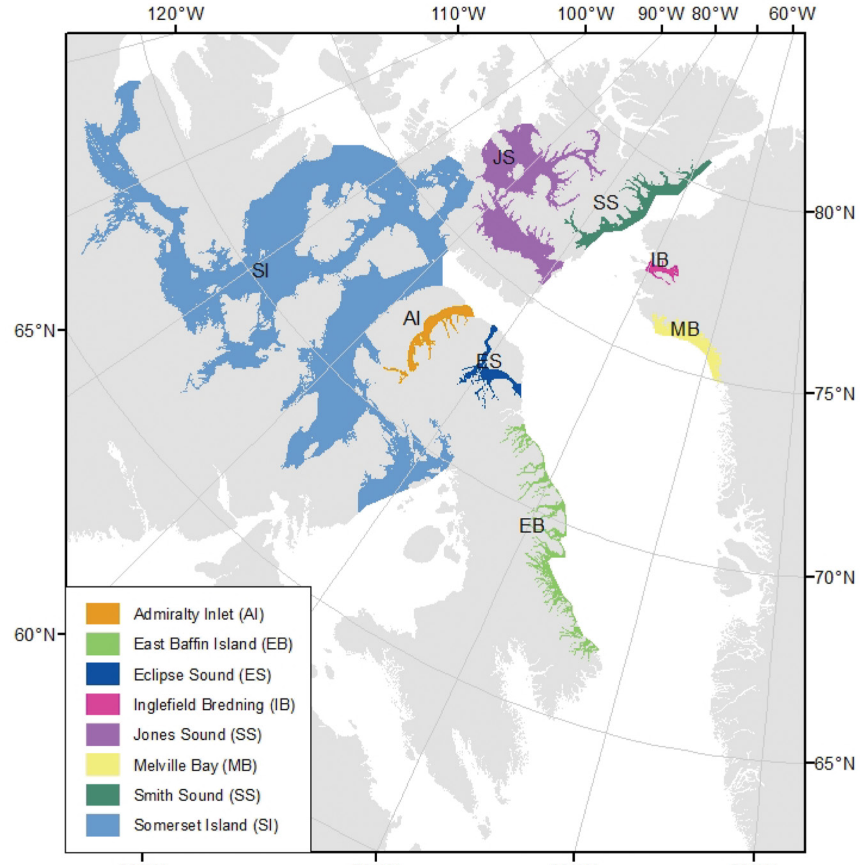

Figure 1.—Summer distribution of narwhal stocks in the Canadian high Arctic and in West Greenland. NSIDC_Sea_Ice_Polar_Stereographic_North projection is used.

sign removals to the stock of origin. In either case, when all takes cannot be assigned positively to a single stock there will be uncertainty in the assignments and a need for a probabilistic assignment scheme.

The Joint Working Group consisting of the North Atlantic Marine Mammal Commission (NAMMCO) Scientific Committee Working Group on the Population Status of Narwhal and Beluga in the North Atlantic and the Canada-Greenland Joint Commission on Conservation and Management of Narwhal and Beluga (JCNB) Scientific Working Group developed a model that estimates the number of animals removed from each stock, using information on movements of each stock to determine which stocks are available to hunters in different hunting areas and seasons. The model has broad application to estimating removals in other migrating marine or terrestrial species impacted by anthropogenic activities (e.g., hunting, exposure to noise, fishery bycatch) in multiple locations and seasons where mixed stocks are present. We developed the model and used it in a case study focused on narwhals.

Narwhals from the Baffin Bay population are part of the subsistence hunt by a number of communities in the Arctic in Canada and Greenland. This population of narwhals is estimated at approximately 140,000 individuals (Doniol-Valcroze et al.[1]), and spends summers in the inlets and fjords of northeastern Canada and western Greenland (Dietz et al., 2001; Heide-Jørgensen et al., 2002, 2003; Laidre et al., 2004; Dietz et al., 2008). Narwhals show site fidelity to their summering region (Heide-Jørgensen et al., 2002, 2003), with nearly all of the few animals tracked by satellite telemetry for a year, returning to the summering aggregation where they were captured (but see Watt et al.[3]). To avoid local depletion, management of the hunt has been based on these individual summer aggregations of the Baffin Bay population, referred to as stocks (Hobbs et al., 2019).

There are six defined narwhal stocks in the Baffin Bay population in northern Canada: the Admiralty Inlet, Somerset Island, Eclipse Sound, East Baffin Island, Smith Sound, and Jones Sound stocks (Doniol-Valcroze et al.[4]) (Fig. 1). In West Greenland there are two defined stocks from the Baffin Bay population: the Melville Bay and Inglefield Bredning stocks (Heide-Jørgensen et al., 2013) (Fig. 1).

Narwhals are hunted in a number of regions across the Canadian Arctic and West Greenland (based on local knowledge; Fig. 2). In Canada, the hunt occurs primarily during summer, but individuals hunted from the Baffin Bay population spend the winter in Davis Strait and Baffin Bay and pass through a number of hunting areas on the migration to and from their summering area (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).

Narwhal stocks have been managed independently of one another, but because of the mixing of stocks during the migration and on the fall and win-

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[3] Watt, C. A., J. Orr, B. LeBlanc, P. Richard, and S. H. Ferguson. 2012. Satellite tracking of narwhals (*Monodon monoceros*) from Admiralty Inlet (2009) and Eclipse Sound (2010-2011). DFO Can. Sci. Advis. Sec. Res. Doc. 2012/046. iii + 17 p. (https://waves-vagues.dfo-mpo.gc.ca/Library/347206.pdf).

[4] 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. 2015/060:v + 36 p. (http://waves-vagues.dfo-mpo.gc.ca/Library/362110.pdf).

ter grounds, a framework that considers stocks to be shared across multiple communities of the two countries was developed to ensure conservation and sustainable management. We present a hunt allocation model that has been applied to narwhal stocks to demonstrate the utility of the model and its ability to inform conservation and management goals for this marine mammal.

Model Development

The stock allocation model assumes that in a region with a hunt from a mixture of stocks, the number of animals taken is proportional to the relative number of individuals from each stock that visit the areas. However, it is often the case that not every animal from a given stock visits the hunting region; i.e., not all individuals from a stock are "available" for the hunt. Probabilities of being taken in the hunt will thus be relative to the portions of each stock that visit the area (instead of their total abundance). Therefore, to allocate removals to the specific stocks, the model requires information on the size of each stock, removals (landed catch plus struck-but-lost) in each hunting region, and the portion of each stock available to hunters in the different locations and seasons. Hunting communities report "landed catch," the number of successfully landed hunted animals; a "struck-but-lost" rate which accounts for animals that were likely killed or severely injured but not recovered and in some cases an "under reporting" rate are applied to the landed catch to estimate total removals (Garde et al., 2019).

Allocation Matrix

The allocation matrix, A, which assigns takes from hunting locations and seasons, is developed in the form of a table with one column for each stock, and rows representing the different areas by season where hunts take place. It is devised so that when transposed and multiplied by a vector of removals by each hunt (area and season) in a year, the number of removals from each stock can be estimated.

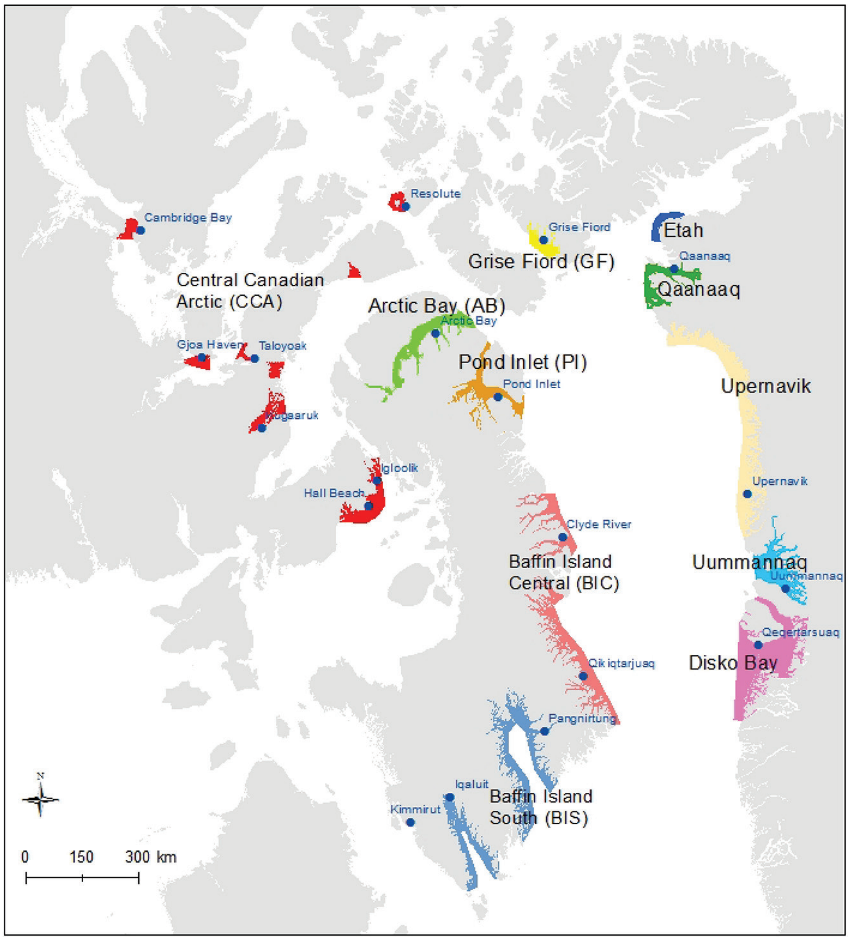

Figure 2.—Harvest locations for narwhal in Canada and Greenland.

Each cell of the allocation matrix, A, has the value:

$$A_{ij} = \frac{P_{ij}N_i}{\Sigma_i P_{ij} N_i}$$

Where,

A_{ij} is the proportion of the jth hunt that is assigned to the ith stock,

P_{ij} is the proportional availability of the ith stock to the jth hunt, an element of the proportional availability matrix, and

N_i is the abundance of the ith stock.

This model assumes that for each stock there is a portion of animals in the stock, between zero and one (P_{ij}), that are 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 A_{ij} should be 1 for each row of the matrix so that all animals taken in the hunt are assigned to stocks since each animal originated from one of the stocks. Note that in areas with hunts from mixed stocks, animals will be split among the stocks because of the uncertainty in the stock of origin. The sum of the P_{ij}, however, does not necessarily add up to 1 in each row because it is the fraction of each stock available to hunters, for instance if half of each of three stocks are available at a location then the sum would be 3/2. Likewise the P_{ij}, does not necessarily add up to 1 in each column because the same stocks can be hunted in several regions over the year and across their migration.

Table 1.— Definitions for the five designations given to each cell in the proportional availability matrix.

Number in text	Designation	Definition
1	Defined zero	Impossible situations such as a summer hunt in a location that was not at a summering ground of the stock, or hunts in areas in other seasons that could not have originated in a particular summering ground based on known movements, e.g., the location was not adjacent to the known migration route wintering ground of the stock.
2	Probable zero	Unlikely to be hunted but proximity during the hunting season could not rule out takes completely.
3	Partial hunt	Data shows a portion of the stock is available to hunters.
4	Probable hunt	Proximity between the stock location and hunting region makes movement or migration to the hunting region almost certain, but where no data exists yet to confirm that the stock is available at the location.
5	Defined hunt	Hunts of the stock within their known home range or summer distribution.

Proportional Availability

To set up the proportional availability matrix, P, each cell in the matrix, i.e., hunt of a given stock at a location in a season, is given one of five designations (Table 1), using information from satellite tracking data, geography, seasonal timing, and expert opinion or local knowledge. Expert opinion is defined as opinion from those members of the Joint Working Group that have spent a significant proportion of their career studying these animals. The designation determines how the cell is calculated. Designations “1. Defined zero” and “2. Probable zero” indicate that a stock is very likely or certainly unavailable to the hunt. For “3. Partial hunt”, data on structure within the stock suggests that only a portion of the stock is available to a hunt. An example is where data indicate that some animals in a stock travel near shore and others travel far offshore beyond the reach of hunters.

In this example the data (telemetry or other information), and hunter’s knowledge and expert opinion on the area hunted are used to determine the proportional availability of the stock at a hunting site by season. The proportion is calculated as the number of animals from a stock that visit a hunting site during the hunting season (x) divided by the total number of animals from that stock for which there is data (n).

Hunting grounds that are known to have only one stock available in a specific season, such as in the summering ground of the stock, are given a designation of “5. Defined hunt”, and the proportional availability will be 1 for that hunt, with no uncertainty. However, in cases where it is likely that only one stock is available but the information on animal availability is insufficient, then these hunts are designated as “4. Probable hunt.” The distinction between the defined and probable zeros and hunts becomes important in the development of the stochastic allocation matrix described below.

We developed a deterministic version of the model but since there is general uncertainty around the proportional availability in the Partial hunts and some uncertainty also in the Probable zeros and Probable hunts, we also developed a stochastic version of the proportional availability matrix to account for this uncertainty. The deterministic and stochastic matrices P differ in their treatment of the “probable” values, resulting in different versions of the allocation matrix A. In the deterministic or “fixed” version of P, cells with defined (designations 1 and 5 in Table 1) and probable (designations 2 and 4 in Table 1) zeros and hunts are given the value zero or one respectively, and for “3. Partial hunt” the values are calculated from the proportion of animals available in the hunting areas from the tracking data (x/n; as explained above).

In the stochastic version, the defined zeros and hunts are given the values zero and one, respectively, as above, while the proportions for partial hunts (designation 3) as well as probable zeros and hunts (designations 2 and 4) are drawn randomly from beta distributions, with the variance (uncertainty) of the beta distribution increasing with fewer animals with data available or smaller values of the Z parameter (described below). The fixed matrix can be used to provide single value results. The stochastic matrix can be used for sensitivity analysis and risk assessment on its own or with a stochastic vector of abundance estimates or hunt takes.

Quantifying Uncertainty

There are two main sources of uncertainty in the analysis: uncertainty in the proportion of animals from one stock that are available to hunters at a given hunting site (P_{ij}), and errors in stock abundance estimates (N_{it}).

Animal Availability

Uncertainty around the proportion of animals available (P_{ij}) is quantified by assuming that the number of animals observed in a certain area follows a binomial distribution with a sample size equal to the number of animals for which there exists data on availability (n) and a probability equal to the true proportion of the animals in that stock that visit the area. This true proportion is unknown but we assume that the likelihood of any one value follows a beta distribution Beta(x+1, n-x+1) (Johnson and Kotz, 1970) where x is the number of animals that visited the area.

The mean of this distribution is $(x+1)/(n+2)$, which converges towards the mean proportion in the fixed version (x/n) with increasing values of x and n. When no connection is documented between a stock and a hunting ground, we distinguish between connections that are deemed extremely unlikely based on expert opinion and connections that are considered unlikely, but not impossible. The former (“1. Defined zeros” Table 1) are assigned a proportional availability of 0, with no uncertainty. The latter (“2. Probable zeros” Table 1) 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 so that the mean of this distribution is 1/(Z+1) (larger values represent higher certainty i.e., closer to zero). Finally, there is the case of "4. Probable hunt", which is parameterized by a Beta(Z, 1) distribution with mean (Z/Z+1), and represents cases where there are no documented movements, but a strong connection is expected (may be from expert opinion, local knowledge, etc.).

In practice, the parameter Z can be thought of as a hypothetical number of animals for which there is data that would result in no animals visiting a hunting area (i.e., 0/Z number of animals), thus a minimum value for Z would be the number of animals with data to date and higher values would reflect certainty resulting from other sources (such as expert opinion, local knowledge, other data such as unique stable isotope or trace element ratios, etc.). This parameter was used for sensitivity testing of the model, setting Z to be identical for all cells designated as "2. Probable zero" and "4. Probable hunt" assuming Z = 10,000 as the base case (i.e., no uncertainty) which approximates the fixed matrix, to assuming Z as low as the *n* values for each stock.

Table 2.—Fixed availability matrix P_{ij} for narwhals from different summering stocks to different hunting regions (*x/n*; available (x) / total (*n*)) based on telemetry data (CCA: Central Canadian Arctic, BIC: Baffin Island Central, BIS: Baffin Island South; see Fig. 2 for hunt locations). "1. Defined zero", and "5. Defined hunt" are represented by 0 and 1, respectively, while 0* and 1* indicates "2. Probable zero, and "4. Probable hunt". Ratios reflect information from satellite telemetry data.

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

Table 3.—Allocation matrix A_{ij} (with no uncertainty) for narwhals from different summering stocks for different hunting regions (CCA: Central Canadian Arctic, BIC: Baffin Island Central, BIS: Baffin Island South; see Figure 2 for hunt locations) and catches for each region. Note that proportions in each line (each site) sum to 1 (all caught animals have to be allocated to a stock). Catches are multiplied by the corresponding allocation proportions for each site, then summed for each stock to yield total removals.

Hunt	Season	Smith Sound	Jones Sound	Inglefield Bredning	Melville Bay	Somerset Island	Admiralty Inlet	Eclipse Sound	East Baffin Island	Catches
Etah	Spring	1	0	0	0	0	0	0	0	0
Qaanaaq	Summer	0	0	1	0	0	0	0	0	87
Grise Fiord	Spring	0	1	0	0	0	0	0	0	5
Grise Fiord	Summer	0	1	0	0	0	0	0	0	0
Grise Fiord	Fall	0	1	0	0	0	0	0	0	4
Upernavik	Summer	0	0	0	1	0	0	0	0	82
Uummannaq	Fall	0	0	0	0.01	0.99	0	0	0	101
Disko Bay	Winter	0	0	0	0.15	0	0.28	0.58	0	66
CCA	Spring	0	0	0	0	1	0	0	0	1
CCA	Summer	0	0	0	0	1	0	0	0	33
CCA	Fall	0	0	0	0	0.89	0.1	0.01	0	23
Arctic Bay	Spring	0	0	0	0	0.57	0.4	0.02	0	43
Arctic Bay	Summer	0	0	0	0	0	1	0	0	167
Arctic Bay	Fall	0	0	0	0	0	0.94	0.06	0	4
Pond Inlet	Spring	0	0	0	0	0.52	0.37	0.11	0	30
Pond Inlet	Summer	0	0	0	0	0	0	1	0	82
Pond Inlet	Fall	0	0	0	0	0	0.24	0.76	0	58
BIC	Spring	0	0	0	0	0	0	0	1	11
BIC	Summer	0	0	0	0	0	0	0	1	9
BIC	Fall	0	0	0	0	0	0.26	0.2	0.54	143
BIS	Spring	0	0	0	0	0	0	0	1	3
BIS	Summer	0	0	0	0	0	0	0	1	1
BIS	Fall	0	0	0	0	0	0	0.04	0.96	18
BIS	Winter	0	0	0	0	0	0	0.09	0.91	0
Total removals		0	9	87	92	195	270	198	119	971

Inclusion of uncertainty changes P_{ij} from a table with fixed values to a table in which each cell is a random variable (see Tables 2 and 3 for example), and therefore changes the resulting allocation matrix A_{ij} from having fixed values to one where each cell contains a probability distribution (see Fig. 3 and 4 for example). For cells with "1. Defined zero" or "5. Defined hunt", these distributions have essentially zero variance and result in a single value of 0 or 1, respectively. Cells with "2. Probable zero" or "4. Probable hunt" have a distribution with mean equal to the corresponding value in the fixed version of the table, for which variance reflects uncertainty around this value. For these probable cells both mean and variance depend on the value of Z. The maximum value of Z=10,000 results in a distribution nearly identical to "1. Defined zero" or

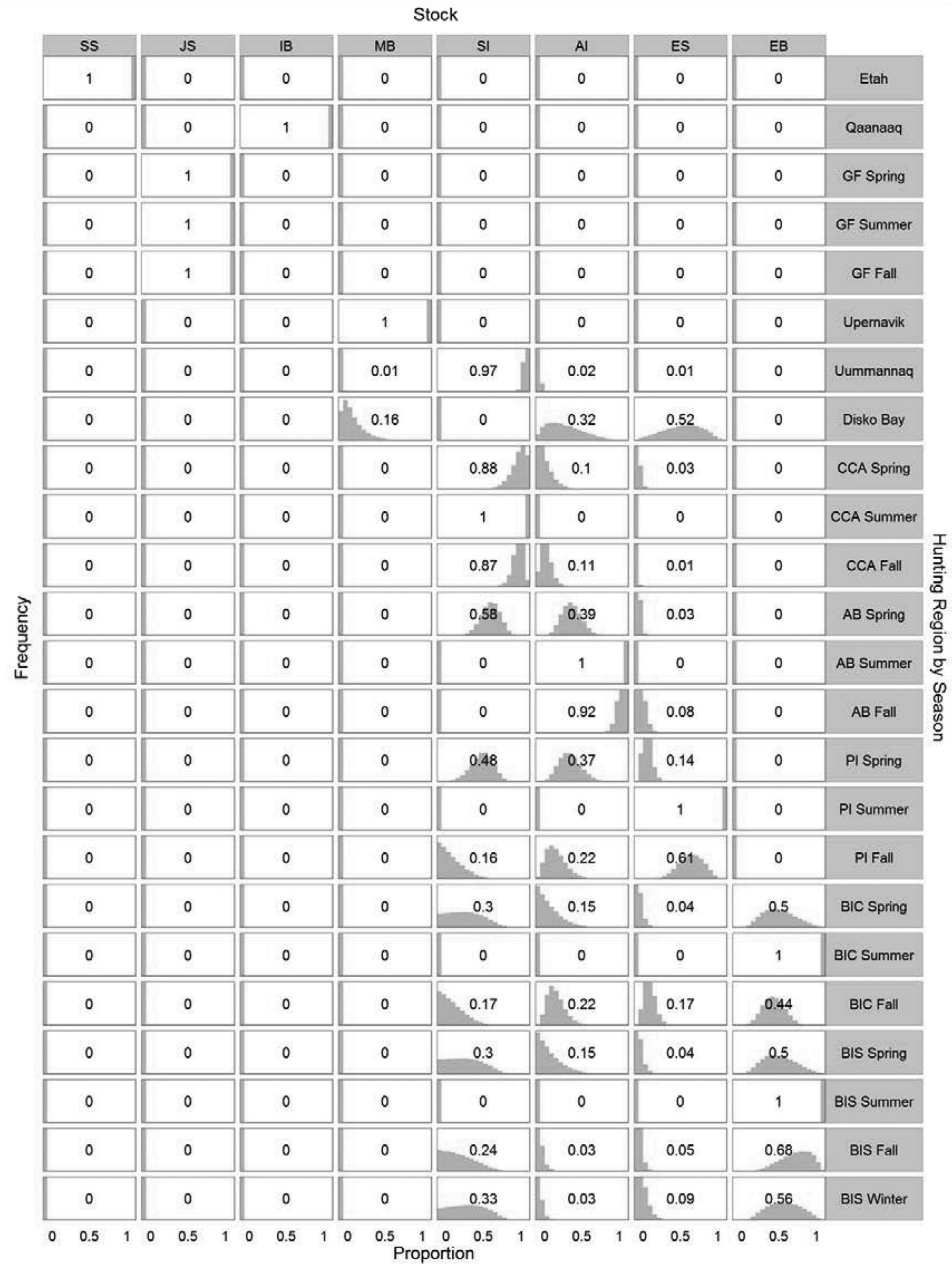

Figure 3.—Allocation matrix A_{ij} with uncertainty in the designation “3. Partial Hunt” but no uncertainty in categories of “2. Probable zero” and “4. Probable hunt” (Z = 10,000). Mean proportions are presented in each cell. Abbreviations are defined in Figures 1 and 2.

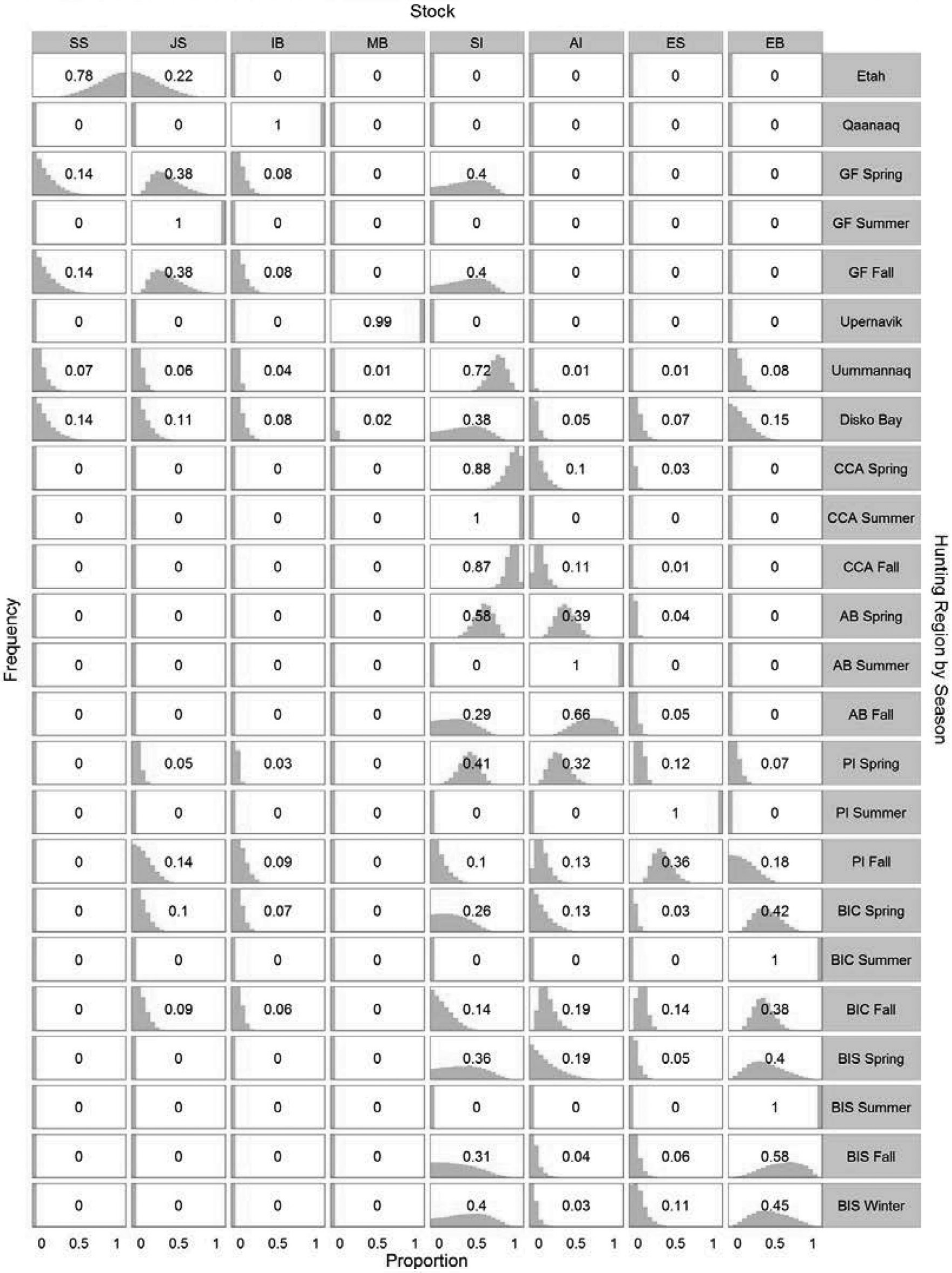

Figure 4.—Allocation matrix A_{ij} with uncertainty in the designation "3. Partial Hunt" and uncertainty in categories of "2. Probable zero" and "4. Probable hunt" (Z = 1). Mean proportions are presented in each cell. Abbreviations are defined in Figures 1 and 2.

Table 4.—Example of removals (and CV%) from each narwhal stock based on the allocation model output for Greenland and Canadian 2013 catches, under several assumptions. Z=10,000 includes uncertainty in the designation “3. Partial hunt” but assumes no uncertainty for “4. Probable zero”, while Z=1 includes maximum uncertainty for “4. Probable zero”. Fixed N assumes no uncertainty in abundance estimates while variable N includes uncertainty in abundance estimates.

Stocks	Smith Sound	Jones Sound	Inglefield Bredning	Melville Bay	Somerset Island	Admiralty Inlet	Eclipse Sound	East Baffin Island
Fixed Allocation Matrix	0	9	87	92	195	271	198	119
Z=10,000 fixed N	0 (46%)	9 (1%)	87 (0%)	93 (7%)	231 (8%)	273 (5%)	183 (8%)	94 (11%)
Z=1 fixed N	19 (46%)	40 (31%)	112 (8%)	84 (1%)	228 (9%)	241 (3%)	135 (5%)	112 (13%)
Z=10,000 variable N	0 (92%)	9 (1%)	87 (0%)	93 (9%)	233 (10%)	271 (12%)	185 (12%)	93 (20%)
Z=1 variable N	18 (70%)	40 (43%)	113 (10%)	84 (2%)	229 (13%)	240 (10%)	136 (10%)	111 (25%)

Table 5.—Removals of narwhal by season (landed catches including estimated struck-but-lost animals) for hunts in Canada and Greenland in 2013 (CCA: Central Canadian Arctic, BIC: Baffin Island Central, BIS: Baffin Island South; see Figure 2 for hunt locations).

Hunt	Season	Removals
Etah	Spring	0
Qaanaaq	Summer	87
Grise Fiord	Spring	5
Grise Fiord	Summer	0
Grise Fiord	Fall	4
Upernavik	Summer	82
Uommannaq	Fall	101
Disko Bay	Winter	66
CCA	Spring	1
CCA	Summer	33
CCA	Fall	23
Arctic Bay	Spring	43
Arctic Bay	Summer	167
Arctic Bay	Fall	4
Pond Inlet	Spring	30
Pond Inlet	Summer	82
Pond Inlet	Fall	58
BIC	Spring	11
BIC	Summer	9
BIC	Fall	143
BIS	Spring	3
BIS	Summer	1
BIS	Fall	18
BIS	Winter	0

“5. Defined hunt”, respectively. Lower values of Z ultimately result in different means and larger coefficients of variation in the allocation matrix (described below in the case study and in Fig. 3 and 4, and Table 4 where we explore Z values of 1 and 10,000).

Abundance

Abundance estimates with given mean (*N*) and coefficient of variation (CV) are assumed to follow a log-normal distribution with parameters μ and σ given by:

$$\mu = \log \frac{N^2}{\sqrt{N^2(1+CV^2)}}$$

and

$$\sigma = \sqrt{\log(1+CV^1)}$$

Monte-Carlo sampling is used to integrate uncertainty in abundance vectors N_{it} in the allocation matrix A_{ijt}. Draw 100,000 samples from a beta distribution for each cell in P_{ij} and 100,000 samples from a lognormal distribution for each value of N_{it} and calculate the value of A_{ijt} for each cell and each sample.

Stock Allocation Model

With the development of the allocation matrix, A_t, the full model is then:

$$S_t = T(A_t)\ H_t$$

Where,

S_t is a vector of the number of narwhal taken in hunts from each stock in year *t*,

$T(A_t)$ is the transposed *A* matrix in year *t*, and

H_t is a vector of the numbers of narwhal taken in hunts at each hunting area by season in year *t*.

As noted above, both A_t and H_t may be stochastic, thus S_t could also be stochastic.

Narwhal Case Study

To highlight the applicability of the model we use an example of narwhal hunted from eight different stocks: Smith Sound, Jones Sound, Inglefield Bredning, Melville Bay, Somerset Island, Admiralty Inlet, Eclipse Sound, and East Baffin Island (Fig. 1), in eleven different regions (Fig. 2) and in multiple seasons in some regions, for a total of 24 hunts.

Removals

For this case study we use landed catch data reported by the hunting communities in Canada and Greenland corrected for struck-but-lost animals in 2013 (Table 5; Watt and Hall[5]). The struck-but-lost factors (landed catches are multiplied by the struck-but-lost factors to estimate total removals) applied to the Arctic Bay, Pond Inlet, and Central Canadian Arctic hunts are 1.35, 1.15, and 1.09, respectively, and are based on loss rates reported by the communities of Arctic Bay, Pond Inlet, and Kugaaruk, Nunavut, Canada, for years between 2005 and 2010 (Watt and Hall[5]). An average struck-but-lost factor of 1.23 determined from these reported communities was used for hunts in Baffin Island Central, Grise Fiord, and Baffin Island South (Watt and Hall[5]). For hunts in Upernavik a factor of 1.15 is used, and for hunts in Etah, Qaanaaq, Ummannaq, and Disko Bay a factor of 1.30 was applied (Garde et al., 2019). The catch data is divided by season to reflect the seasonal availability quantified in the allocation matrix.

Seasonal dates were defined based on narwhal movements in and out of the summering region for Canada and Greenland. For Greenland, spring was defined as 1 April–9 August, summer as 10 August–22 September, fall as 12 September–31 October, and winter as 1 November–31 March. For the Canadian catch data, spring was defined from 1 April–23 July, summer as 24 July–24 August, fall as 25 August–30 November, and winter as 1 December–31 March.

Abundance

The most recent abundance estimate for each stock from aerial surveys that

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[5] Watt, C. A., and P. Hall. 2018. Catch statistics for narwhal (*Monodon monoceros*) in Canada from 1970-2015. Can. Tech. Rep. Fish. Aquat. Sci. 3270:vi + 209 p. (http://waves-vagues.dfo-mpo.gc.ca/).

have accounted for perception and availability bias is presented in Table 6 (Heide-Jørgensen et al., 2010; Doniol-Valcroze et al.[4]; Hansen et al.[6]).

Table 6.—The most recent abundance estimates with CVs and 95% confidence intervals (CI), estimated using the log-based method described by Buckland et al. (2001), for the eight narwhal stocks.

Stock	Year	Abundance estimate	CV	95% CI
Smith Sound	2013	16,360	0.65	5,110–52,373
Jones Sound	2013	12,694	0.33	6,760–23,838
Inglefield Bredning	2007	8,368	0.25	5,165–13,558
Melville Bay	2014	3,091	0.50	1,225–7,802
Somerset Island	2013	49,768	0.20	33,758–73,371
Admiralty Inlet	2013	35,043	0.42	15,904–77,214
Eclipse Sound	2013	10,489	0.24	6,596–16,679
East Baffin Island	2013	17,555	0.35	9,017–34,179

Table 7.—Stochastic availability matrix P_{ij} for narwhals from different summering stocks to different hunting regions (x/n; available (x) / total (n)) based on telemetry data (CCA: Central Canadian Arctic, BIC: Baffin Island Central, BIS: Baffin Island South; see Fig. 2 for hunt locations). 0 and 1 are fixed values, but ratios follow beta distributions ($\alpha = x+1$; $\beta = n-x+1$), all ratios for which $n=Z$ are sensitive to changes in Z. Other ratios reflect information from satellite telemetry data.

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	0	0	1	0	0	0	0
Uummannaq	Fall	0/Z	0/Z	0/Z	1/9	1	0/42	0/26	0/Z
Disko Bay	Winter	0/Z	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

Proportional Availability and Allocation Matrices

There are eight columns in the proportional availability and allocation matrices for narwhals that represent the individual summer stocks (Fig. 1). Twenty-four rows represent the hunting grounds (Fig. 2) divided by season where applicable; thus, for each stock and hunt there is a cell in the matrix. The value in each cell of the availability matrix was determined based on satellite telemetry data for narwhals collected over the last 25 years by both Canada and Greenland and expert opinion and local knowledge about the connection among stocks and hunting regions based on the designations 1–5 defined in Table 1.

A fixed version of the availability matrix defines "2. Probable zero" and "4. Probable hunt" as 0 and 1, respectively (Table 2). When applied to the abundance estimates, this yields a fixed version of the allocation matrix (Table 3). Catches are applied to the corresponding allocation proportions for each site, then summed for each stock to yield total removals. However, when uncertainty is considered, each cell contains a probability distribution, and a stochastic version of the proportional availability matrix for narwhals is produced (Table 7). The resulting distributions in the allocation matrix include uncertainty in both the proportional availabilities of narwhals and abundance estimates for the individual stocks (Fig. 3 for Z=10,000 and Fig. 4 for Z=1). The effect of adding uncertainty in abundance estimates on removals from each stock, for different values of Z, is shown in Table 4 and Figure 5. Since there are many cells designated as "2. Probable zero" for East Baffin Island, as uncertainty increases (lower values of Z) the takes from this stock go up since the probability that whales are taken from this stock in other hunting areas goes up (it is less likely that the true value is zero; Fig. 5 with distributions shown in Fig. 3 and 4).

Alternatively, for Admiralty Inlet there are no "2. Probable zero" or "4. Probable hunt" cells, but as Z decreases the uncertainty in the beta distribution for cells designated as "3. Partial hunt" goes up (or uncertainty in what the true proportion of the population available to hunters in other areas goes up). In this case, this results in the total take going down slightly (Fig. 5) since the true proportion for that stock goes down (Fig. 3 and 4). This reduction is particularly driven by the connection identified between Disko Bay and the Admiralty Inlet stock since only one of 42 tagged narwhals travelled into the Disko Bay hunting region. When uncertainty about whether this one whale represents a true proportion of the Admiralty Inlet stock available to hunters in Disko Bay goes up, the proportion of the catches allocated to that stock changes from 0.32 (Fig. 3) to only 0.05 (Fig. 4). The R code for running this model is provided in Supplementary Appendix A with the example narwhal data in Supplementary Appendix B.

Discussion

The model can allocate hunted animals to specific stocks for each hunting season and site by incorporating information on animal movements and migration, which is essential for

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[6] 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. R. Hansen, Greenland Institute of Natural Resources c/o Greenland Representation, Strandgade 91, 2. sal, 1401 København K, Denmark.

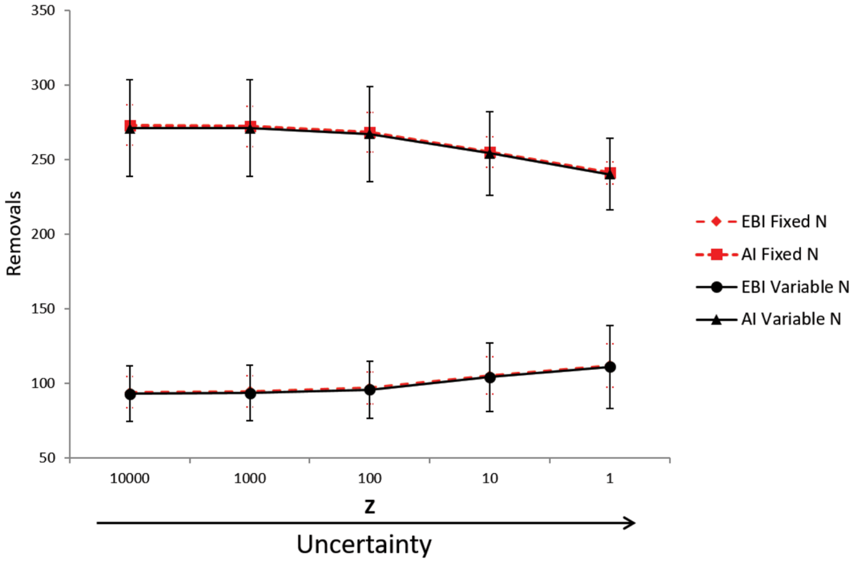

Figure 5.—An example of the effect of the uncertainty parameter Z and uncertainty in abundance estimates on removals (± SD) from the Admiralty Inlet (AI) and East Baffin Island (EBI) stocks, based on allocation of Greenland and Canadian catches from 2013. Fixed N assumes no uncertainty in abundance estimates while Variable N includes uncertainty in abundance estimates. Uncertainty increases as Z decreases in cells with a designation of "2. Probable zero".

sustainable stock management (Ogburn et al., 2017). The model output can be improved with increased information on animal movements, which may mean increased satellite tagging efforts, or quantification of other movement indices (chemical tracers, sampling and analysis of DNA from hunted whales, local knowledge, etc.). With limited information on some of the stocks in the narwhal case study, the model output relies on local knowledge and expert opinion, and the sensitivity analysis shows how changes in these parameters impact the catch allocations and suggests incorporation of uncertainty is critical for stocks for which little movement information is available. The model can easily be adapted for use for other hunted or fished species and provides a pathway for incorporating movement information into conservation and management (Allen and Singh, 2016; Ogburn et al., 2017). For use on other species, sensitivity analysis of the chosen Z value is important and model users will need to decide the level of certainty they are comfortable with since changes to the Z value impact removals for individual stocks.

For the narwhal case study, the success of the model for managing stocks relies on international collaboration between Canada and Greenland. By combining information about narwhal movements through sharing of telemetry data, abundance estimates, expert opinion, and local knowledge from both countries we are able to have a more meaningful and comprehensive view of the situation. If the model is to be adapted for other hunted animals, we strongly suggest that incorporation of data from all geographic areas where the animal migrates is needed to ensure the model is capturing all data and uncertainty that exists across the species range. Harrison et al. (2018) evaluated movement data from 14 species of marine predators in relation to geopolitical boundaries and found that all of the species evaluated entered numerous jurisdictions, highlighting the need for international management. Conservation of many of the species evaluated will require collaboration among many countries and regions within a country (Harrison et al., 2018). Our modeling framework provides one method for evaluating stock overlap and is a successful example of international co-management.

In the narwhal case study, even with collaboration between nations and sharing of data, there is uncertainty in the data and subsequent model output. Telemetry data does not exist for all the narwhal stocks, and for those that have movement information, there is not uniform coverage of different geographical areas or seasons. Although all stocks have an abundance estimate, trends in abundance are unavailable for some stocks or are based on relatively few data points and it is uncertain how this could affect the model results (e.g., future loss of sea ice could result in changes in seasonal narwhal movements that may result in changes to abundance estimates for specific stocks and this may not be captured accurately without frequent abundance estimates).

Catch statistics may not be precise; in particular the struck-but-lost rate which is applied may not be accurate for all hunt types in different seasons, which may result in an over or under estimate of the total catches. Struck-but-lost rates specific to different hunting regions would be beneficial and would allow incorporation of uncertainty in this parameter for the different stocks. Finally, although the model can allocate catches to the different stocks, it is unknown how management decisions (e.g., to which season to allocate most catches) may influence stock sustainability in the long run.

Despite the limitations of the model used here, this framework provides a direct link between movement information and management policy. Gathering animal telemetry data is costly and ecologically interesting but is often not used to directly impact conservation and policy decisions (McGowan et al., 2017). The framework presented here can be used to identify data gaps, and allow for prioritization of research specific to stocks for which there exists high uncertainty about movement.

Through evaluation of the management implications and how decisions may change with more or less certainty about movements, researchers and managers can evaluate the pros (improved management) and cons (financial investment) of acquiring more telemetry data (McGowan et al., 2017). Management of hunted animals often only considers part of the life cycle or life history of the animal and ignores movement into other management jurisdictions (Ogburn et al., 2017). This model bridges that gap and can allow for a more complete understanding of the life history of the animal, ultimately leading to more sustainable management. Few examples of hunt management based on movement data exist in the literature, but a banding study on mallard ducks by Nichols et al. (1995) evaluated patterns of geographic variation in harvest rates, essentially using movement as a method to measure harvest reporting and gain information on harvest statistics. Similarly, by using reported harvest and movement data together to allocate catches, the model presented here can directly inform management decisions. The model presented here is only as good as the data that goes into it and an understanding of animal movement across all seasons and throughout its geographical range is needed for it to be successful. This model can only allocate catches to specific stocks after they have occurred, and thus, hunt allocation or setting of future quotas for the different hunts is the next step (see Witting et al., 2019).

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