

# Evaluating critical dispersal rates for whale management under the IWCs Revised Management Procedure: An application for North Atlantic common minke whales

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## ABSTRACT

A key consideration for any Revised Management Procedure (RMP) and Aboriginal Whaling Management Procedure (AMWP) *Implementation* is the choice of stock structure hypotheses, and the weighting of alternative stock structure hypotheses using available data. The RMP/AWMP-lite framework is applied to the North Atlantic common minke whales for three stock structure hypotheses and two RMP ‘variants’. The stock structure hypotheses differ in terms of how many stocks are found in the North Atlantic and how they mix on the feeding grounds. Focusing on the eastern North Atlantic, simulations are undertaken to assess when management performance for two RMP variants is inadequate and how much effective dispersal between adjacent stocks is needed so that the performance of these variants becomes adequate.

KEYWORDS: WHALING; MANAGEMENT; NORTH ATLANTIC; MINKE WHALES

## INTRODUCTION

The management strategies (or management procedures) applied by the International Whaling Commission (IWC) to determine catch (or strike) limits for commercial and aboriginal subsistence whaling are selected by means of simulation (the management strategy evaluation approach). This process involves a number of steps (Punt and Donovan, 2007):

- (1) identification of management goals (and performance measures to quantify the extent to which those goals are achieved);
- (2) selection of hypotheses that pertain to the situation at hand, and development of operating models that represent those hypotheses—the set of operating models forms the ‘trials structure’;
- (3) conditioning of the operating models on the available data (and possible rejection of hypotheses [or combinations of hypotheses] that are not compatible with the data);
- (4) identification of candidate management strategies; and
- (5) simulation of the performance of the management strategies against agreed objectives by projecting the operating model forward in which catch limits are set using the management strategy.

A wide range of uncertainties are considered in the trials that are used to evaluate management strategies for whale populations. However, the two uncertainties that have consistently proved to be most challenging in terms of management strategies achieving conservation objectives, while still achieving goals related to high and stable catches (commercial whaling) and satisfying aboriginal need

(aboriginal subsistence whaling) are the productivity of the resource usually quantified through the exploitation rate at which maximum sustainable yield rate [MSYR] is achieved, and the number of stocks in the area being managed and how they mix.

It is well known that managing multiple stocks as if they are a single stock can lead to a failure to achieve conservation objectives (e.g. Dougherty *et al.*, 2013; Fu and Fanning, 2004; IWC, 1992; Martien *et al.*, 2013; Spies, 2014). Therefore, information on stock structure can be important for the purpose of management. However, it is rarely the case that stock structure can be resolved with certainty. Uncertainty regarding stock structure and its implications for management under the IWC’s Revised Management Procedure (RMP) and Aboriginal Whaling Management Procedure (AWMP) has therefore been a considerable focus for discussion during meetings of the Scientific Committee of the IWC, and the IWC Scientific Committee has attempted to adopt an approach to selecting stock structure hypotheses that makes use of genetic and non-genetic data (Donovan, 1991). A trials structure that allows for multiple stocks has been developed for the North Atlantic common minke whales, *Balaenoptera acutorostrata* (IWC, 1993), the Bering-Chukchi-Beaufort Seas bowhead whales, *Balaena mysticetus* (IWC, 2008a), the western North Pacific Bryde’s whales, *Balaenoptera edeni* (IWC, 2008b), the North Atlantic fin whales, *Balaenoptera physalus* (IWC, 2009) and the western North Pacific minke whales, *Balaenoptera acutorostrata* (IWC, 2014).

The performance of a management strategy in terms of achieving conservation objectives when stock structure is uncertain depends on the management strategy being evaluated. For example, management strategies that aim for lower exploitation rates and that spread catches spatially are

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more likely to outperform strategies that allow for higher exploitation rates and that allow catches to be taken from a small fraction of the area being managed (IWC, 1992; Spies, 2014). Conservation performance will be better when there are multiple stocks if there is dispersal<sup>3</sup> among them because this provides an opportunity for a ‘rescue effect’ (Brown and Kodric-Brown, 1977). Thus, the need to understand stock structure (from a management perspective) is much reduced if there is high dispersal between stocks.

The statistical power of neutral genetic tests for stock structure relies on the sample size and the degree of genetic differentiation, measured using genetic distance metrics such as  $F_{ST}$  among stocks (Taylor and Dizon, 1996). Genetic differentiation at neutral loci is influenced by the level of gene flow between stocks, which is a product of the migration rate (the probability  $m$  that an individual is a migrant) and the effective population size ( $N_e$ ). When gene flow is restricted, genetic drift will promote genetic divergence. As a result, detecting stock structure using genetic approaches is straightforward when dispersal is limited (Mills and Allendorf, 1996; Taylor and Dizon, 1996). For example, variation in microsatellite markers in the Pacific cod, (*Gadus microcephalus*), has revealed a strong pattern of isolation by distance, suggesting restricted gene flow and considerable self-recruitment among populations in the northeastern Pacific (Cunningham *et al.*, 2009). Limited dispersal of Pacific cod was also detected between the Aleutian Islands and the eastern Bering Sea using a landscape genetics approach (Spies, 2012), leading to the reappraisal of the Aleutian Islands and eastern Bering Sea management unit (Spies, 2014). However, low genetic differentiation, e.g. due to ongoing or recent gene flow, reduces statistical power in genetic studies. This is problematic for detecting stocks, because the amount of dispersal required to achieve genetic homogeneity is often lower than the dispersal rate below which stocks should be assigned to different management units (Shaklee and Bentzen, 1998; Waples, 1998). The problem of low statistical power could be solved by investing in genotyping more individuals and/or increasing the number of genetic markers. However, it is seldom clear *a priori* how many samples or markers will be adequate to determine whether there are multiple stocks in a proposed management unit.

The aim of this paper is to develop a framework that integrates uncertainty regarding stock structure and rates of mixing<sup>4</sup> and dispersal amongst stocks within a management context. The aim of the framework is to identify levels of dispersal for which (conservation) performance is adequate, and can hence be used in studies of power to assess sample sizes for genetic studies (Palsboll *et al.*, 2007). The work is embedded within the actual management system because the critical level of dispersal will depend on the management system and how it addresses uncertainty, for example, regarding stock structure. The framework is applied for illustrative purposes to the situation of managing common

minke whales in the North Atlantic using the IWC’s Revised Management Procedure (RMP)<sup>5</sup>.

## METHODS

### Outline of approach

The analyses in this paper are based on the RMP/AWMP-lite framework. This framework involves developing operating models using a general modelling structure to allow rapid evaluation of whether hypotheses are likely comparable with the data and the likely performance of candidate management strategies. In particular, RMP/AWMP-lite is based on representing populations using age- and sex-aggregated population dynamics models, and allows for scenarios in which multiple stocks are found in the region to be managed. RMP/AWMP-lite allows for dispersal among stocks, as well as mixing of stocks on the feeding grounds. Nevertheless, the framework could be applied with other types of population dynamics models (age- and sex-structured) commonly used when testing management strategies for the IWC, although at perhaps severe computational cost.

The approach for selecting the critical level of dispersal is as follows:

- (1) select a set of stock structure hypotheses and a set of candidate management strategies (the critical dispersal rate will depend on the stock structure hypothesis and the management strategy);
- (2) condition the stock structure hypotheses on the data (i.e. fit the operating model to the available monitoring data) for the lowest plausible value for MSYR (the conservation performance of a management strategy will be poorer for this value MSYR);
- (3) identify ‘problematic’ combinations of management strategies and stock structure hypotheses<sup>6</sup> by conducting projections where the level of dispersal among stocks is set to zero (the worst case scenario); and
- (4) conduct additional projections for the ‘problematic’ combinations in which dispersal is allowed between adjacent stocks and the level of dispersal is increased until the results are no longer ‘problematic’.

It is possible that for a particular management strategy that there is no level of dispersal at which conservation performance is adequate. Such a strategy is too aggressive and does not warrant being considered further.

### RMP/AWMP-LITE

The population dynamics are based on the Pella-Tomlinson model, i.e.:

$$N_{t+1}^i = N_t^i + r^i N_t^i \left(1 - [N_t^i / K^i]^d\right) - C_t^i \quad (1)$$

<sup>5</sup>The specifications and definition of terms for the RMP can be found in IWC (2012b).

<sup>6</sup>‘Problematic’ combinations are those that lead to failure to achieve the conservation-related goals of the IWC. For this paper, a combination of stock structure hypothesis and management strategy is considered ‘problematic’ if the lower 95<sup>th</sup> percentile of final depletion for any stock is less than the (assumed) MSY level of 0.6, although criteria such as those used to define adequate conservation performance under the RMP (IWC, 2012a) could have been adopted instead. However, this paper is primarily illustrative and the approach of IWC (2012a) can be quite computationally intense.

<sup>3</sup>The term ‘dispersal’ is used here in the sense of ‘effective dispersal’ and refers to permanent movement of individuals among stocks. Such individuals become part of the population to which they move and contribute to future reproduction.

<sup>4</sup>‘Mixing’ is defined here as two stocks which overlap at some time on the feeding groups but do not interbreed.

where  $N_t^i$  is the number of stock  $i$  animals at the start of year  $t$ ;  
 $K^i$  is the carrying capacity of stock  $i$ ;  
 $r^i$  is the intrinsic rate of growth for stock  $i$ ;  
 $z^i$  is the degree of compensation (selected so that  $\text{MYSL}^1$  – the population size at which MSY is achieved for stock  $i$  – equals a pre-specified value); and  
 $C_t^i$  is the catch during year  $t$  from stock  $i$ .

The number of animals in stock  $i$  at the start of the first year of the model forecast ( $y_{\text{init}}^i$ ) is  $N_{y_{\text{init}}}^i = \delta^i K^i$ . The catch by stock is determined by apportioning the catches by area, taking account of mixing (i.e. exposure to harvesting) matrices, according to:

$$C_t^i = \sum_A C_t^A \frac{X^{A,i} N_t^i}{\sum_j X^{A,j} N_t^j} \quad (2)$$

where  $C_t^A$  is the catch in area  $A$  during year  $t$ ; and  
 $X^{A,i}$  is the relative exposure of stock  $i$  to harvesting in area  $A$  (i.e. the proportion of stock  $i$  in area  $A$  when catches are taken) – the catch mixing matrix.

Dispersal can be modelled under the assumption of no net movement of animals between stocks at carrying capacity, i.e.:

$$N_{t+1}^i \leftarrow N_{t+1}^i (1 - l_{i-j}) + \lambda_{i-j} \frac{K^j}{J^j} N_{t+1}^j \quad (3)$$

where  $l_{i-j}$  is the dispersal rate between stocks  $i$  and  $j$ .

The values for the parameters of the population dynamics model are: (a) the intrinsic rate of growth by stock, (b) the stock-specific carrying capacities, (c) the ratio of the number of animals at the start of the modelled period to carrying capacity (if treated as estimable), (d) the dispersal rates and (e) the values for the entries of the catch mixing matrices. The fourth of these quantities must be pre-specified by the user for the purposes of this paper, while the values for the remaining parameters can either be pre-specified or estimated by minimising an objective function<sup>7</sup>. In principle, dispersal rates can be estimated if data on tagging (genetic or non-genetic) are available, but the need to use the framework of this paper is lower in these cases given a key source of information on movement is available.

The contribution of the estimates of abundance to the objective function is:

$$L_1 = \sum_A \sum_t \frac{(\ln \hat{B}_t^A - \ln B_t^{A,\text{obs}})^2}{2\sigma_t^A} \quad (4)$$

where  $B_t^{A,\text{obs}}$  is the abundance estimate for area  $A$  and year  $t$ ;  
 $\hat{B}_t^A$  is the model-estimate of the abundance corresponding to  $B_t^{A,\text{obs}}$ .

$$\hat{B}_t^A = \sum_i \tilde{X}^{A,i} N_t^i \quad (5)$$

<sup>7</sup>The values for the parameters of AWMP/RMP-lite can be estimated by fitting the model to mixing proportions by area, minimum abundance estimates and tagging data (Punt, 2013), but those data are not available for the North Atlantic minke whales.

$\sigma_t^A$  is the standard error of the logarithm of  $B_t^{A,\text{obs}}$ , and  
 $\tilde{X}^{A,i}$  is the relative exposure of stock  $i$  when surveys taken place in area  $A$  (i.e., the proportion of stock  $i$  in area  $A$  when surveys are undertaken) – the sightings mixing matrix.

The projections are based upon the assumption that survey estimates of abundance become available on a pre-specified frequency. A removal limit for each area is set as a catch limit from the RMP tuned to achieve a median final depletion for the ‘D1’ trial of 0.72 (see IWC, 2012b). The CV for future surveys is assumed to be 0.25 for the illustrative analyses of this paper.

### Application to North Atlantic common minke whales

#### Specifications: Operating models

The *Implementation* for the North Atlantic common minke whales was completed in 1993 (IWC, 1994) based on operating models specified in IWC (1993). Two *Implementation Reviews* have been conducted for this group of whales (in 2003 and 2008; see IWC, 2004; IWC, 2009)) and an *Implementation Review* is currently being undertaken (IWC, In press). The *Implementation Simulation Trials* for the North Atlantic minke whales are described in IWC (1993). Those trials involved ten sub-areas in the North Atlantic with three stocks (‘W’, ‘C’ and ‘E’), each of which consists of sub-stocks (2 for the ‘W’ stock (‘WC’ and ‘WG’), 4 for the ‘C’ stock (‘CIP’, ‘CG’, ‘CIC’ and ‘CM’), and 4 for the ‘E’ stock (‘EN’, ‘EC’, ‘ES’, and ‘EB’))<sup>8</sup>. The sub-areas on which the original trials were based (Fig. 1a) were modified during the 2003 *Implementation Review* to those in Fig. 1b, but the trials were not revised (IWC, 2004). The trials documented in IWC (1993) considered some variants of these basic stock structure hypotheses:

- (1) sub-stock ‘CM’ is part of the ‘E’ stock;
- (2) sub-stock ‘EN’ is a separate stock, sub-stocks ‘WC’, ‘WG’, ‘CIP’, ‘CG’, ‘CIC’ and ‘CM’ are components of one (‘C’) stock, and sub-stocks ‘EC’, ‘ES’, and ‘EB’ are components of one (‘E’) stock; and
- (3) sub-stock ‘CIP’ is part of the ‘W’ stock.

The original *Implementation Simulation Trials* considered values for  $\text{MSYR}_{\text{mat}}^9$  of 1% and 4%, two levels of current abundance, and various scenarios regarding catch and sightings mixing. Unlike the original *Implementation Simulation Trials*, there are now sufficient data points (Table 1) to estimate the sub-stock carrying capacities by fitting (conditioning) the operating model on the data. Only one scenario regarding  $\text{MSYR}_{1+}^{10}$  is considered in this paper because it is well-known that the RMP performs adequately when  $\text{MSYR}_{\text{mat}} = 4\%$  (IWC, 1993; 2008a; 2008b; 2009; 2014).  $\text{MSYR}$  in Equation 1 pertains to the total population size rather than mature component of the population. Consequently,  $\text{MSYR}$  is set to 0.66% in this paper to roughly mimic  $\text{MSYR}_{\text{mat}} = 1\%$ <sup>11</sup>.  $\text{MSYL}_{1+}$  is assumed to be 0.6,

<sup>8</sup>A new sets of trials is currently under development (IWC, In press) that include trials with one, two and three stocks, as well as a scenario of two cryptic stocks.

<sup>9</sup> $\text{MSYR}$  defined in terms of harvesting of mature animals only.

<sup>10</sup> $\text{MSYR}$  defined in terms of harvest of all animals aged 1 and older.

<sup>11</sup>De la Mare (2014) questions a simple relationship between  $\text{MSYR}_{1+}$  and  $\text{MSYR}_{\text{mat}}$  but this assumption is adequate for the purposes of this paper.

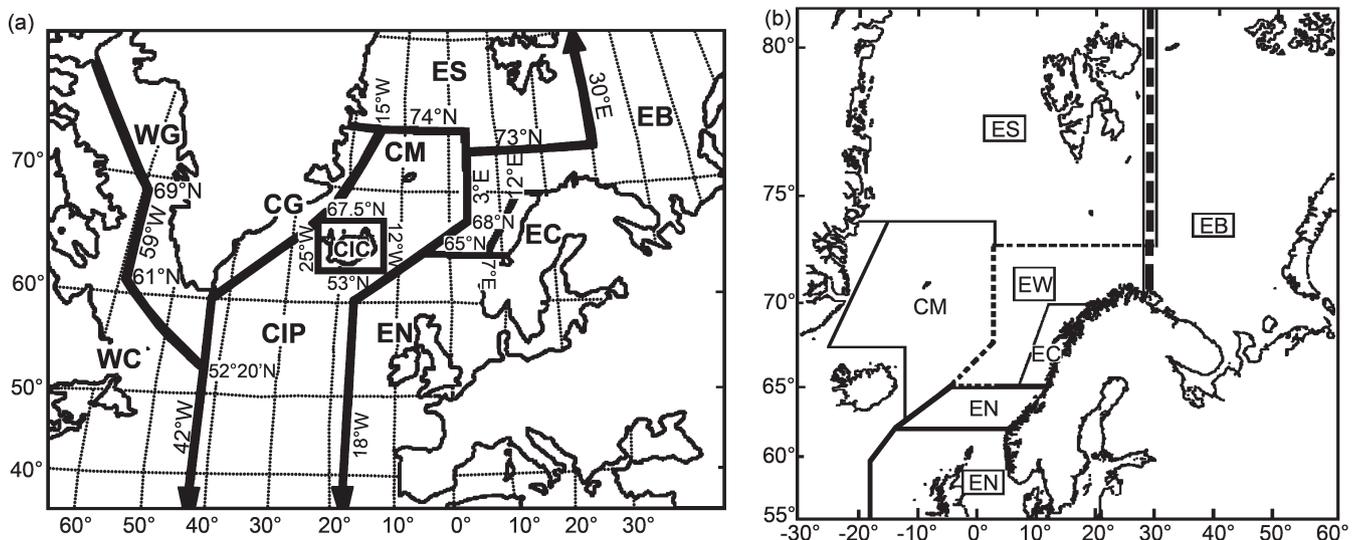


Fig. 1. Map of the North Atlantic outlining the ten sub-areas included in the original trials (left panel) and as the eastern area was modified during the 2003 Implementation Review (right panel).

Table 1  
Abundance estimates used for conditioning.

Sub-area	Year	Estimate	CV	Sub-area	Year	Estimate	CV
WC	2007	20,741	0.30	EB	1989	21,868	0.21
WG	1993	8,370	0.43	EB	1995	29,712	0.18
WG	2005	10,790	0.59	EB	2000	25,885	0.24
WG	2007	16,100	0.43	EB	2007	28,625	0.23
CIP	2007	1,350	0.60	EN	1989	8,318	0.25
CG	2007	1,048	0.38	EN	1995	22,536	0.23
CIC	1987	24,532	0.32	EN	1998	13,673	0.25
CIC	2001	43,633	0.19	EN	2004	6,246	0.47
CIC	2007	10,680	0.29	ES	1989	13,070	0.13
CM	1988	4,732	0.229	ES	1995	24,891	0.10
CM	1995	12,043	0.28	ES	1999	17,406	0.14
CM	1997	26,718	0.14	ES	2003	19,377	0.28
CM	2005	26,739	0.45	EW	1989	20,991	0.17
				EW	1995	34,986	0.12
				EW	1996	23,522	0.13
				EW	2005	27,152	0.22

Table 2

Catch and sightings mixing matrix for stock structure hypothesis A. X denotes that the stock concerned can be found in the sub-area indicated by the column header.

Stock	Sub-area									
	WC	WG	CIP	CG	CIC	CM	EN	EC	ES	EB
W	X	X*	0	0	0	0	0	0	0	0
C	0	0	X	X*	X*	X*	0	0	0	0
E	0	0	0	0	0	0	X	X*	X*	X*

\*Indicates an estimable parameter of the catch/sightings mixing matrix (there is one fewer parameter for each stock than the number of sub-areas in which a stock is found because the entries of a mixing matrix for a stock must sum to one).

$y_{init} = 1938$ , and each stock is assumed to be at its unfished level at the start of 1938 (i.e. = 1).

This paper is based on a small set of (example) alternative stock structure hypotheses that might form the basis for future *Implementation Simulation Trials*. These are summarised below:

(1) Stock Structure Hypothesis A. There are three stocks (and no sub-stocks), the catch and sightings mixing

matrices are assumed to be same (Table 2), with the parameters determining the proportion of each stock in each sub-area estimated (along with the carrying capacities by stock) to mimic the abundance estimates;

(2) Stock Structure Hypothesis B. There are ten stocks<sup>12</sup>, each stock is in 'their' sub-area when catches and sightings occur (Table 3a); and

(3) Stock Structure Hypothesis C. There are ten stocks, each stock is in 'their' sub-area when catches occur (i.e. the catch mixing matrix is diagonal), but they are mixed on the feeding grounds when surveys take place (Table 3b).

#### Specifications: RMP variants

Only two RMP variants<sup>13</sup> are considered in these analyses primarily because the focus for these calculations was the performance of the RMP for the sub-stocks that constitute the eastern stock. The RMP variants are defined as follows:

<sup>12</sup>Mimicking a situation in which there are three stocks but each stock consists of a number of sub-stocks.

<sup>13</sup>RMP variants are specifications for how stock structure uncertainty will be addressed – they involve different ways to spread catches spatially. See IWC (2012b) for definitions for 'catch cascading', 'combination areas', etc.

Table 3  
Sightings mixing matrices for the stock structure hypotheses B and C.

Sub-stock	Sub-area									
	WC	WG	CIP	CG	CIC	CM	EN	EC	ES	EB
<b>(a) Stock structure hypothesis B</b>										
WC	1	0	0	0	0	0	0	0	0	0
WG	0	1	0	0	0	0	0	0	0	0
CIP	0	0	1	0	0	0	0	0	0	0
CG	0	0	0	1	0	0	0	0	0	0
CIC	0	0	0	0	1	0	0	0	0	0
CM	0	0	0	0	0	1	0	0	0	0
EN	0	0	0	0	0	0	1	0	0	0
EC	0	0	0	0	0	0	0	1	0	0
ES	0	0	0	0	0	0	0	0	1	0
EB	0	0	0	0	0	0	0	0	0	1
<b>(b) Stock structure hypothesis C</b>										
WC	0.5	0.5	0	0	0	0	0	0	0	0
WG	0	1	0	0	0	0	0	0	0	0
CIP	0	0	0.45	0.1	0.25	0.2	0	0	0	0
CG	0	0.1	0.2	0.4	0.3	0	0	0	0	0
CIC	0	0	0.05	0.03	0.87	0.05	0	0	0	0
CM	0	0	0.25	0.1	0.25	0.4	0	0	0	0
EN	0	0	0	0	0	0.2	0.75	0.05	0	0
EC	0	0	0	0	0	0	0.15	0.8	0.05	0
ES	0	0	0	0	0	0.2	0.05	0.2	0.45	0.1
EB	0	0	0	0	0	0	0.05	0.35	0.05	0.55

- (1) Sub-area ‘CIC’ (Iceland) is treated as a *Small Area*, and sub-areas ‘EN’, ‘EC’, ‘ES’ and ‘EB’ are treated as a *Combination Area*, with ‘catch cascading’ applied across these four sub-areas; and
- (2) Sub-area ‘CIC’ (Iceland) is treated as a *Small Area*, and sub-areas ‘EN’, ‘EC’, ‘ES’ and ‘EB’ are treated as a *Small Area*, with all of the catch taken from sub-area ‘EB’.

RMP variant (2) can be considered to be the most risky so it is the focus for the analyses.

*Specifications: Calculating dispersal*

The trials are initially conducted with no dispersal amongst the stocks. The output from these trials is then used to determine the distribution of stock size relative to carrying capacity in year 100 (final depletion) and hence the probability that the depletion is 0.6 or higher. ‘Failure’ is considered to occur when this probability is less than 0.95. Dispersal between the ‘ES’ and ‘EB’ sub-stocks is then implemented and the extent of dispersal increased until the probability that final depletion is 0.6 or higher exceeds 0.95. The choice of sub-stock ‘ES’ is arbitrary and was chosen here for illustrative purposes.

**RESULTS**

**Model fits**

Fig. 2 shows the fit of the operating model to the abundance estimates for the three example stock structure hypotheses. In terms of likelihood, the 3-stock operating model (hypothesis A, which, because it estimates mixing proportions, see Table 2, has the same number of parameters as the 10-stock operating models) has the lowest negative log-likelihood (47.9), although the fit is only marginally better than that of the 10-stock operating model with no mixing (stock structure hypothesis B; negative log-likelihood of 48.6). In contrast, the negative log-likelihood of the operating

model that includes mixing (stock structure hypothesis C) is 60.1 (Fig. 2). The poor fit of stock structure hypothesis C is evident in the fits to the abundance estimates for sub-areas ‘WG’, ‘CIP’ and ‘EN’. Poor fits to the abundance data are perhaps not unexpected for this stock structure hypothesis given that the mixing rates were selected ‘by expert judgement’ rather than by fitting the model to any data.

**Projections (no dispersal)**

Fig. 3 shows time-trajectories of stock size relative to carrying capacity for the ‘E’ stock for the 3-stock operating model and for the four easternmost sub-stocks for the two 10-stock operating models for the two RMP variants. The remaining stocks are never depleted to be below 60% of carrying capacity after 100 years. The solid line is the median over simulations while the shading covers 90% of the distributions.

The performance of both RMP variants is adequate when there are no sub-stocks (see Fig. 3, upper panels). Similarly, the performance of catch cascading is adequate for the two 10-stock stock structure hypotheses except for sub-stock ‘EW’ under RMP variant 1 (lower panels of Fig. 3). However, the performance of RMP variant 2 is poor for the ‘EB’ sub-stock, irrespective of whether there is or is not mixing on the feeding grounds when surveys take place.

The poor performance of RMP variant 1 for the ‘EW’ sub-stock when there is mixing on the feeding grounds when surveys take place occurs because even if the ‘EW’ sub-stock is extirpated, the estimates of abundance for the ‘EW’ sub-area do not reflect this. Consequently, the RMP allocates catches to sub-area ‘EW’ even though there are no animals in this sub-area when catches occur (Figs 3 and 4). The poor performance of RMP variant 2 occurs because all of the catch occurs in the ‘EB’ sub-area even though the catch limit is based on the abundance estimates for the entire ‘E’ management area.

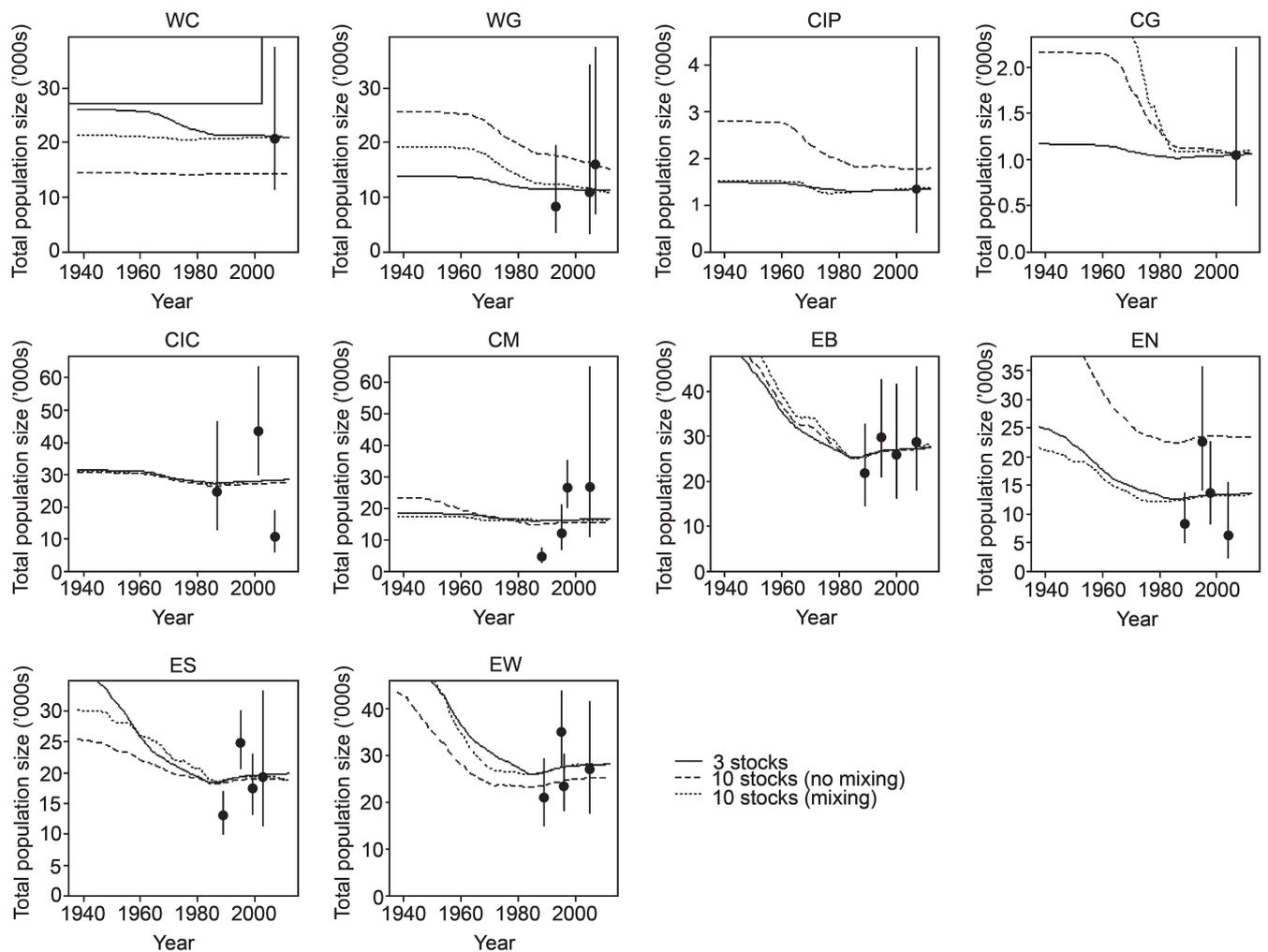


Fig. 2. Fits of the three operating model variants to the abundance data.

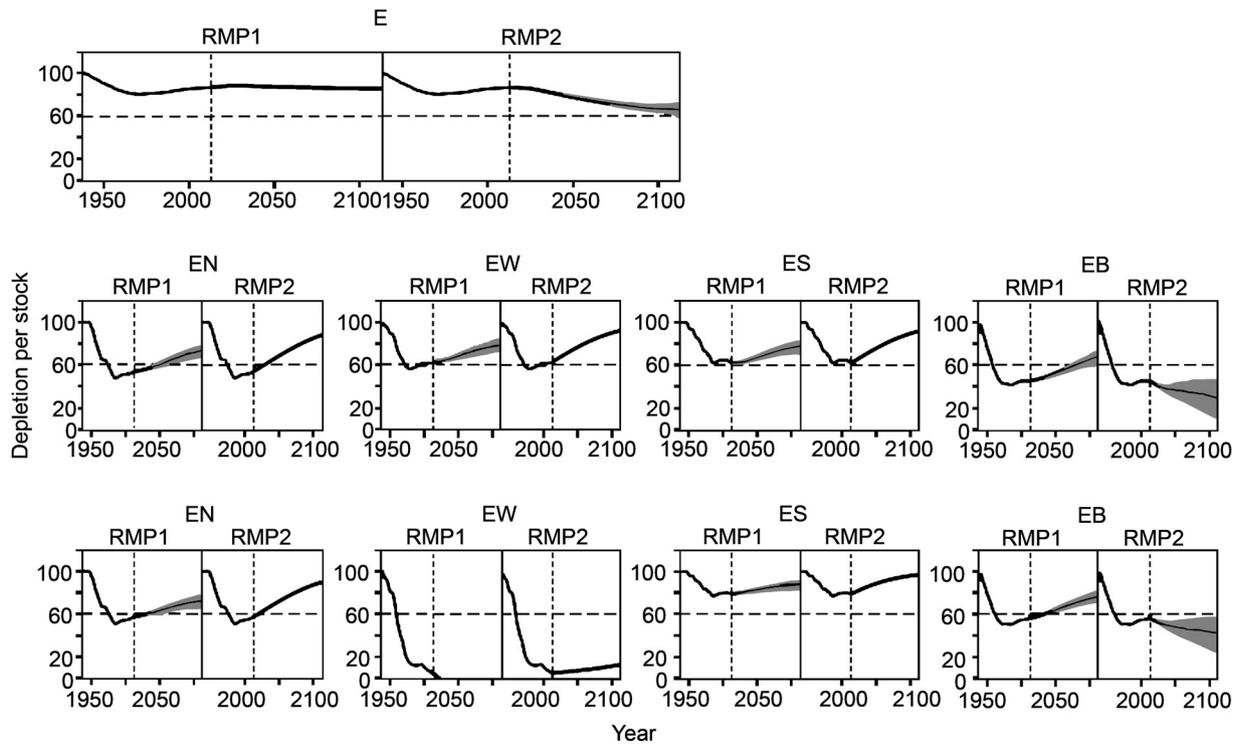


Fig. 3. 100-year time-trajectories of 1+ abundance relative to carrying capacity based on projections for the three operating models (upper panels: Stock structure hypothesis A; centre panels: Stock structure hypothesis B; lower panels: Stock structure hypothesis C). Results are shown for the two RMP variants. The light line denotes the historical estimates of abundance and the solid line the median of the forecasts in each panel, while the shaded area encompasses 90% of the simulated future trajectories.

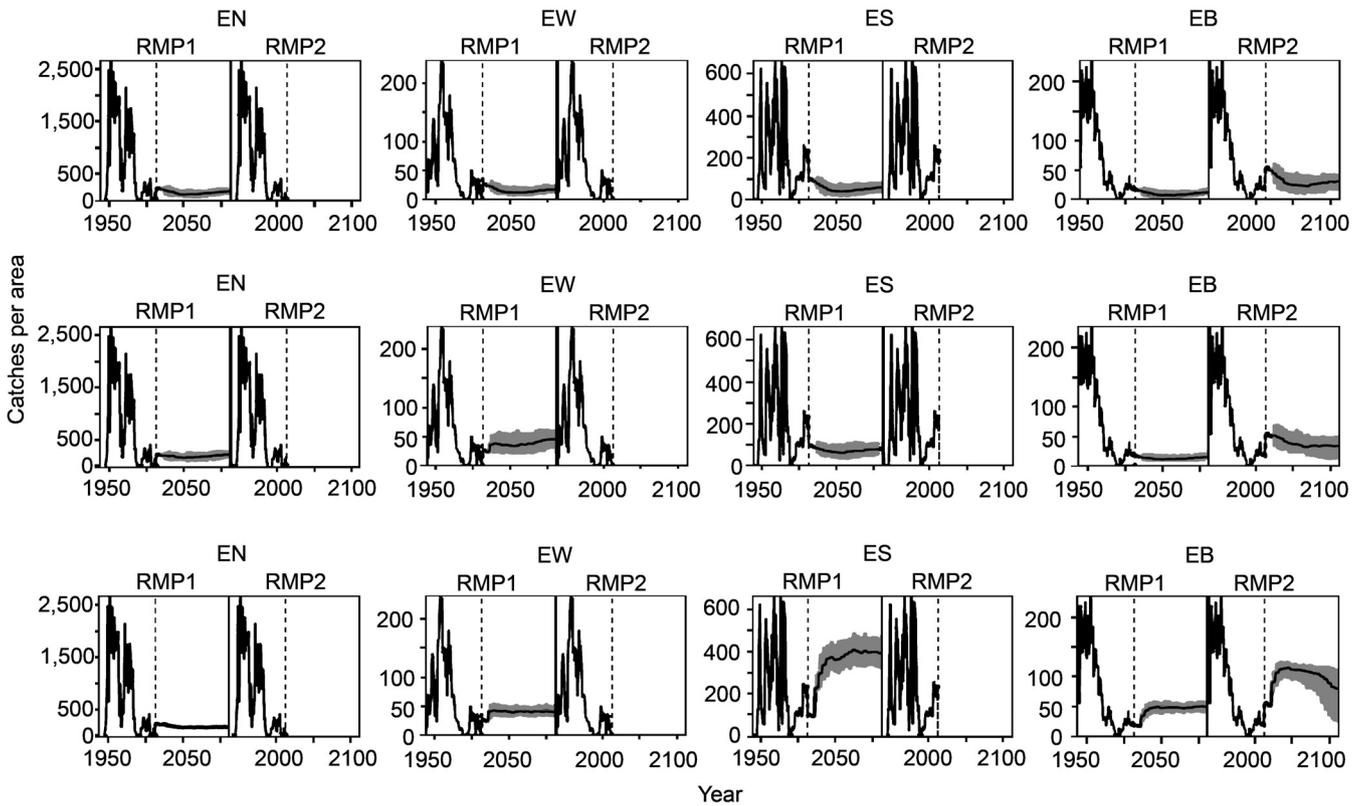


Fig. 4. Catches per area for the three operating models (upper panels: Stock structure hypothesis A; centre panels: Stock structure hypothesis B; lower panels: Stock structure hypothesis C). Results are shown for the two RMP variants. The light line denotes the historical catches and the solid line the median of the forecasts in each panel, while the shaded area encompasses 90% of the simulated future trajectories of catch.

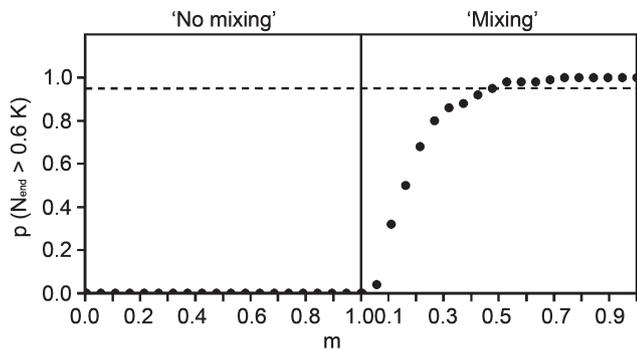


Fig. 5. The probability of final depletion being higher than 0.6 versus dispersal rate for stock structure hypotheses B ('no mixing') and C ('mixing') under RMP variant 2. The dashed line indicates the threshold value  $p = 0.95$ .

**Projections (with dispersal)**

Fig. 5 shows the probability of RMP variant 2 satisfying the risk criterion that the probability that the final (year 100) depletion is 0.6 or higher exceeds 0.95 as a function of the rate of dispersal between sub-stocks 'ES' and 'EB'. This goal is achieved for a dispersal rate of 0.05 when there is mixing during sightings surveys (see the right panels of Figs 5 and 6). However, there is no dispersal rate that allows the risk criterion to be satisfied when there is no mixing during surveys and RMP variant 2 is applied (Fig. 5, left panel).

**DISCUSSION**

This paper outlines how RMP/AWMP-lite can be used to evaluate the consequences of different stock structure hypotheses given different RMP variants, and to assess the

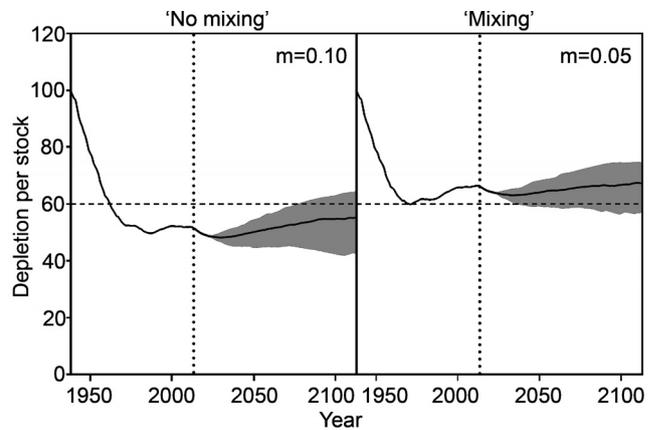


Fig. 6. Depletion trajectories for sub-stock EB at which management performance becomes adequate (or closest to adequate) for stock structure hypotheses B ('no mixing') and C ('mixing') under RMP variant 2. For stock structure hypothesis B the highest explored value of dispersal rate is shown. The light line denotes the historical estimates of abundance and the solid line the median of the forecasts, while the shaded area encompasses 90% of the simulated future trajectories.

level of dispersal among areas, that may be consequential for management purposes. The results of the paper (and extended calculations based on alternative stock structure hypotheses/RMP variants) should help the process of conducting the *Implementation Review* for the North Atlantic common minke whales and other future *Implementations* and *Implementation Reviews* in at least three ways:

- (1) Some RMP variants (e.g. variant 2 in this paper) may be unacceptable for all levels of dispersal for some stock structure hypotheses. In these cases, the RMP variant is

not a feasible candidate for implementation and does not need to be examined further, in particular using complex *Implementation Simulation Trials*;

- (2) Assumptions regarding when mixing takes place are consequential. In particular, the poor performance of catch cascading for sub-stock 'EW' (lower row of Fig. 3) can be attributed almost totally to the assumption that there is mixing when surveys take place but not when catches occur. Those designing the trials structure need to consider whether this is a valid assumption; and
- (3) The results in Fig. 5 provide a threshold level of mixing that should form the basis for evaluations of the power of genetic methods to detect population structure. However, the level of dispersal suggested is probably undetectable under most practical genetic analyses.

On a broader scale, the methodology described in this paper demonstrates the potential of species-specific demographic simulation frameworks, such as RMP/AWMP-lite, for assessing demographic independence in the context of pre-defined management goals. Solid genetic criteria for management units can be developed by determining the level of genetic divergence at the level of dispersal at which management performance is adequate. In addition, the number of genetic markers required to resolve population structure can be assessed upfront, which allows for an efficient targeted approach. This also prevents the waste of valuable conservation resources if the expected level of genetic divergence is too low to be detected by population genetic approaches and improves the integration of genetics into the management toolkit.

## ACKNOWLEDGEMENTS

Partial funding for this work was provided through financial support from the International Whaling Commission to André Punt and Per Palsbøll. Robin Waples and an anonymous reviewer are thanked for their comments on an earlier version of this paper.

## REFERENCES

- Brown, J. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecol.* 445–49.
- Cunningham, K., Canino, M.F., Spies, I.B. and Hauser, L. 2009. Genetic isolation by distance and localized fjord population structure in Pacific cod (*Gadus macrocephalus*): limited effective dispersal in the northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* 66: 153–66.
- De La Mare, W. 2014. The relationship between  $MSY_{mat}$  and  $MSY_{1+}$  based on energetics modelling. 17pp [Received]. Paper SC/65b/RMP04 presented to the IWC Scientific Committee, May 2014, Bled, Slovenia (unpublished). 17pp. [Paper available from the Office of this Journal].
- Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn (special issue)* 13: 39–68.
- Dougherty, D.T., Hilborn, R., Punt, A.E. and Stewart, I.J. 2013. Modeling co-occurring species: a simulation study on the effects of the spatial scale for setting management targets. *Can. J. Fish. Aquat. Sci.* 70: 49–56.
- Fu, C.H. and Fanning, L.P. 2004. Spatial considerations in the management of Atlantic cod off Nova Scotia, Canada. *N. Am. J. Fish. Manage.* 24: 775–84.
- Hauser, L. and Carvalho, G.R. 2008. Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. *Fish Fish.* 9: 333–62.
- International Whaling Commission. 1992. Report of the Third Comprehensive Assessment Workshop on Management Procedures, Oslo, 1–8 February 1990. *Rep. int. Whal. Commn* 42:271–304.
- International Whaling Commission. 1993. Report of the Scientific Committee, Annex I. Report of the Working Group on Implementation Trials. *Rep. int. Whal. Commn* 43:153–96.
- International Whaling Commission. 1994. Report of the Scientific Committee, Annex D. Report of the Sub-Committee on Management Procedures. *Rep. int. Whal. Commn* 44:74–92.
- International Whaling Commission. 2004. Report of the Scientific Committee, Annex D. Report of the Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 6:75–184.
- International Whaling Commission. 2008a. Report of the Scientific Committee, Annex E. Report of the standing working group on the development of an aboriginal subsistence management procedure. *J. Cetacean Res. Manage. (Suppl.)* 10:121–49.
- International Whaling Commission. 2008b. Report of the Scientific Committee, Annex D. Report of the sub-committee on the Revised Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 10:90–120.
- International Whaling Commission. 2009. Report of the Scientific Committee, Annex D. Report of the sub-committee on the Revised Management Procedure (RMP). *J. Cetacean Res. Manage. (Suppl.)* 11:91–144.
- International Whaling Commission. 2012a. Requirements and Guidelines for Implementations under the Revised Management Procedure. *J. Cetacean Res. Manage. (Suppl.)* 13:495–506.
- International Whaling Commission. 2012b. The Revised Management Procedure (RMP) for Baleen Whales. *J. Cetacean Res. Manage. (Suppl.)* 13:483–94.
- International Whaling Commission. 2014. Report of the Scientific Committee, Annex D1. Report of the Working Group on the Implementation Review for Western North Pacific Common Minke Whales. *J. Cetacean Res. Manage. (Suppl.)* 15:112–88.
- International Whaling Commission. In press. Report of the Scientific Committee, Annex D. Report of the Sub-Committee on the Revised Management procedure (RMP). *J. Cetacean Res. Manage.* 16 (Suppl.).
- Martien, K.K., Gregovich, D.P. and Punt, A.E. 2013. Defining the appropriate 'Unit-To-Conserve' under the International Whaling Commission's Revised Management Procedure. *J. Cetacean Res. Manage.* 13(1): 31–38.
- Mills, L.S. and Allendorf, F.W. 1996. The one-migrant-per-generation rule in conservation and management. *Conserv. Biol.* 10: 1,509–18.
- Palsboll, P.J., Berube, M. and Allendorf, F.W. 2007. Identification of management units using population genetic data. *Trends Ecol. Evol.* 22(1): 11–16.
- Punt, A.E. 2013. Application of RMP/AWMP-lite to North Atlantic fin whales. Paper SC/65a/RMP05 presented to the IWC Scientific Committee, June 2013, Jeju Island, Republic of Korea (unpublished). 15pp. [Paper available from the Office of this Journal].
- Punt, A.E. and Donovan, G.P. 2007. Developing management procedures that are robust to uncertainty: lessons from the International Whaling Commission. *ICES J. Mar. Sci.* 64: 603–12.
- Shaklee, J.B. and Bentzen, P. 1998. Genetic identification of stocks of marine fish and shellfish. *Bull. Mar. Sci.* 62: 589–621.
- Spies, I. 2012. Landscape Genetics Reveals Population Subdivision in Bering Sea and Aleutian Islands Pacific Cod. *Trans. Am. Fish. Soc.* 141: 1,557–73.
- Spies, I. 2014. Building a bridge between genetics and fisheries management; addressing loss of genetic diversity, the utility of small datasets, and mismatches between management and biological units. PhD thesis, University of Washington [Available from the University of Washington].
- Taylor, B.L. and Dizon, A.E. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. *Mol. Ecol.* 8: S11–S16.
- Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *J. Hered.* 89: 438–50.