Managing a complex population structure: exploring the importance of information from fisheries independent sources

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Abstract

Natural resource managers aim to manage fish stocks at sustainable levels. In a number of cases, management of these stocks is based on the results of analytical stock assessments. Accurate catch data, that can be attributed to a specific population unit and reflects the population structure, is needed for these approaches. Often though, the quality of the catch data is compromised when dealing with a complex population structure where fish of different population units mix in a fishery. The herring population units west of the British Isles are prone to mixing. Here, the inability to perfectly allocate the fish caught to the population unit they originate from, due to classification problems, poses problems for management. These mixing proportions are often unknown; therefore, we use simulation modelling combined with Management Strategy Evaluation to evaluate the role fisheries independent surveys can play in an assessment to provide unbiased results, irrespective of population unit mixing and classification success. We show that failure to account for mixing is one of the major drivers of biased estimates of population abundance, affecting biomass reference points and MSY targets. When mixing of population units occurs, the role a survey can play to provide unbiased assessment results is limited. Either different assessment models should be employed or stock status should be considered from the survey data alone. In addition, correctly classifying the origin of fish is especially important for those population units that are markedly smaller in size than other units in the population complex. Without high classification success rates, smaller population units are extremely vulnerable to over-exploitation.

Keywords

Atlantic Herring, British Isles, classification, *Clupea harengus*, FLR, management strategy evaluation, mixing, stock structure, scientific survey

1. Introduction

Managing economically important fish stocks at sustainable levels is the aim of natural resource managers (FAO, 1999; Reiss *et al.*, 2009). This can be achieved either by pursuing a fishery at Maximum Sustainable Yield (Mace, 1994; UN, 2002) or through the development of management plans tested to be robust against natural variability of the resource and the uncertainty in sampling it (Kell *et al.*, 2007; Punt and Donovan, 2007).

In a number of cases, however, sustainable management is hampered by a mismatch between the scale of a biological population and that of the realised management unit (Iles and Sinclair, 1982; Stephenson, 1999; Frank and Brickman, 2000; Reiss *et al.*, 2009; Cope and Punt, 2011; Ulrich *et al.*, 2013). For example, monitoring local population units, rather than a population as a whole, is necessary to maintain resilience, genetic diversity and spawning potential (Kerr *et al*., 2010; Payne, 2010; Harma *et al*., 2012). Additionally, population units that mix at different life stages in their life cycle pose problems for providing accurate advice (Stephenson, 1999; Kell and Bromley, 2004; Campbell *et al*., 2007; Kell *et al*., 2009). The latter problem arises because the spatial definition of a unit stock, possibly created for political and management convenience (Stephenson, 1999; Smedbol and Stephenson, 2001), is not always identical to the biological definition of a population unit. Here, the concept of a population or population unit, defined on primarily biological characteristics, might be markedly different from the concept of a stock, created for management purposes. It is therefore possible that catches, in many cases the main data source for assessment driven advice, might originate from more than one population unit (Geffen *et al.*, 2011) thereby violating the assumption of a single stock assessment (Hart and Cadrin, 2004).

To bridge the gap between complex population structure and stock assessment model assumptions, complex (assessment) models have been developed and scenario tested (Porch *et al*., 2001; Andrews *et al*., 2006; Yakubu and Fogarty, 2006; Cunningham *et al*., 2007; Heath *et al*., 2008; Kell *et al*., 2009; Kerr *et al*., 2010). These models are especially valuable to evaluate hypotheses on population or stock structure and dynamics

(Hilborn, 2003; Kerr *et al.*, 2010) and provide insight into the most sustainable management actions. Management Strategy Evaluation (MSE) (Kell *et al.*, 2007; Kraak *et al.*, 2008) is another tool to investigate the implications of the mismatch between complex population structure and assumed stock assessment units. In order to derive results directly applicable to management, more emphasis should be placed on modelling biological/operational realism and estimation of uncertainty associated with these processes (Butterworth *et al.*, 2010). Many studies do incorporate empirically derived data on life history traits (Begg *et al*., 1999; Kritzer and Sale, 2004; Kerr *et al*., 2010). However, historical records of data such as catch time series are rarely used to set up starting conditions for model simulations. Estimated trends in abundance and mortality based on historical records can indicate the boundaries to conditions such as mixing. These boundaries should ensure that assumed mixing proportions do not go beyond the point where movement of fish from one to another area exceeds the size of the source population. Part of correcting for mixing relates to re-examining or monitoring the productivity (measured as recruit per spawner) of population units, which are most often seen as drivers of population development (Heath *et al.*, 2008; Secor *et al.*, 2009).

Other than catch data, fisheries independent data could play an important role in the sustainable management of complex population structures (Beare *et al.*, 2005; Cope and Punt, 2011; Mesnil *et al.*, 2009). In only a few cases, however, have management implications associated with fisheries independent information collection been simulated (Simmonds, 2009). These data sources could support alternative ideas on managing complex population structures, although survey catch, similar to fisheries catch, might also consist of population unit mixtures. A straightforward evaluation approach is to embed the survey sampling and population unit classification process into the MSE framework. One assumption in the MSE is that population units can be correctly classified within the survey and therefore true population unit mixing in the survey indices is known. This setup allows testing of the influence of such a survey in assessments, while the catch data is not corrected for potential population unit mixing

Here, an MSE framework has been developed to study the added value of fisheries independent surveys in a management context. The herring (*Clupea harengus*) population complex to the west of the British Isles is used as a case study. The population complex consists of three major spawning units and each unit is separately managed as a stock in ICES areas VIaN, VIaS/VIIb,c and VIIaN (Figure 1). The units have been found to mix (i.e. multiple units physically occurring in the same location) during the feeding season (Campbell *et al.*, 2007; Geffen *et al.*, 2011). This mixing takes place during the summer and mainly in ICES area VIaN, across the Hebrides and Malin shelves (Figure 1). It is expected that the fisheries which operate outside of the spawning season (autumn and winter) catch a mixture of population units, but the absolute mixing proportion is unknown. Acoustic surveys are carried out during the summer months. Since 2008, one synoptic survey ($\text{acoustic}_{\text{I}}$) has covered ICES areas VIIb, VIaS and VIaN and another separate acoustic survey ($\text{acoustic}_{\text{II}}$) has covered ICES area VIIaN since 1989. The current surveys are used by ICES as tuning indices for the VIaN ($\text{acoustic}_{\text{I}}$) and VIIaN ($\text{acoustic}_{\text{II}}$) stocks and in exploratory assessments for herring in VIaS/VIIb,c ($\text{acoustic}_{\text{I}}$). The $\text{acoustic}_{\text{I}}$ survey catches a mixture of the different population units and is currently not split by unit. Since 2009, however, the $\text{acoustic}_{\text{I}}$ survey (herein referred to as the Malin Shelf survey) has been sampled to enable the indices to be split by unit and potentially correct for unit mixing in the survey indices. The Malin Shelf survey design is here used within the MSE simulations. The VIaN ICES stock assessment is tuned with the $\text{acoustic}_{\text{I}}$ survey where the survey data are representative of more than one, currently unquantified, population unit (Hatfield *et al.*, 2007). The VIaS/VIIb,c stock is assessed by ICES using catch data and with additional exploratory assessments carried out which include $\text{acoustic}_{\text{I}}$ survey data. The VIIaN ICES assessment utilises catch data and the $\text{acoustic}_{\text{II}}$ survey data. A management plan is in place for VIaN herring (Council Regulation (EC) No. 1300/2008). A rebuilding plan has been proposed for herring in VIaS/VIIb,c and a management plan is under development for herring in VIIaN.

In this study, the ICES stock assessment data (ICES, 2012a) are taken directly as input to the simulations to improve operational realism and represent best available knowledge on the population complex. To simplify the simulations the ‘southern stock’ in the Celtic Sea and south of Ireland (ICES areas VIIaS,g,j,h,k) is not included. In order to avoid getting embroiled in the argument about defining a metapopulation (Levins, 1969; Hanski, 1998; Kritzer and Sale, 2004) we will continue to consider the complex as a series of population units (see Smedbol *et al.*, 2002) where, for instance, fish that spawn in the Irish Sea (VIIaN) are considered to be a different population unit from the fish that spawn to the north and west of Ireland (in VIaS and VIIb,c) or north and west of Scotland (in VIaN) (see Figure 1). The combination of all population units together is considered here as the population complex.

In a fishery and survey where different population units are caught simultaneously, proportions by unit or spawner type, such as autumn and winter spawners, can be identified to improve the data that support management actions (Gröger and Gröhsler, 2001; Bierman *et al*., 2010). However, in situations where population units mix that are morphologically or genetically similar, such as in the Malin Shelf survey, it is difficult to accurately allocate fish to population units. Consequently, misclassifications might result in a biased pattern in either the catch or the survey indices. Methods have been developed to determine the population origin accurately e.g., otolith microstructure (Clausen *et al.*, 2007), otolith microchemistry (Geffen *et al.*, 2011), otolith shape analyses (Burke *et al*., 2008; Cadrin *et al*., 2013) and parasite prevalence methods (Campbell *et al.*, 2007). For any of these methods, when examined individually, in the west of the British Isles study (the WESTHER project, (Hatfield *et al.*, 2007)) a maximum classification success rate within the sampled spawning aggregations of around 0.8 was achieved. There is, therefore, still a level of uncertainty in the allocation of individuals or groups of individuals (catches or samples) to their putative population unit or stock.

This study focuses on the survey design of a population complex, and the success of resulting management advice on stock level when fisheries and survey catches contain mixtures of population units. Mixing proportions of population units are known only in a few cases; accurately splitting survey indices by population unit, an exercise not executed for fisheries catch, could contribute to a lower bias in assessment abundance estimation. Here, the effects of varying classification success rates and sample sizes taken in surveys on the accuracy of the stock assessment are evaluated. The extent of population unit mixing is varied to contrast the fishery independent results to the uncertain nature of population unit mixing. The use of MSE allows us to investigate if sustainable management of the population units is possible when dealing with catch mixtures and classification issues in the fisheries independent survey. Results shown here indicate marginal improvement in stock management under improved survey design under the current assessment model setup. The analyses do show, however, the importance and consequences of acquiring unbiased fisheries data. These results are relevant in designing management plans that take population unit mixing and uncertainties in monitoring into account.

2. Material & Methods

The MSE framework considers five components (2.1 – 2.5): the biological population units of herring to the west of the British Isles, each spawning within three respective ICES areas: VIaN, VIaS/VIIb,c and VIIaN (Figure 1) [2.1], the three different fisheries targeting these populations [2.2], the collection of fisheries independent data based on surveys [2.3], the stock assessment procedure to identify the perceived status of the three population units [2.4], and the procedure to set fishery management targets [2.5]. These procedures include feedback loops where, over time, the outcomes of management actions affect the population units the year after which, in its turn, affects the fishery and management. The simulations are run with 100 Monte Carlo realisations, and hence error structures, as described below, are also different per realisation. These repetitions are used to evaluate the range in outcomes and risk of certain management scenarios to over-exploitation. Simulations were run until the year 2025 while the time series started in 1970 and simulation commenced in 1999 (see 2.1 for a more detailed explanation). A mathematical description of the simulation framework is given in the supplementary material while key equations are also embedded within the text below.

In the simulation framework, the operating model simulates the dynamics of the three population units. This is contrasted with stock dynamics represented by the stock assessment model based on catch and survey data. These data sources may contain mixed or mis-specified data from multiple population units.

2.1 Population units

Current perceptions of herring population units for management purposes

To the west of the British Isles there are a number of putative herring stocks which are recognised on an area basis to constitute separate managed ‘stocks’ (ICES, 1994). The five stocks recognised by ICES are VIaN (“West of Scotland”), VIaS/VIIb,c (“West of Ireland and Porcupine Bank”), the “Irish Sea” (VIIaN), the “Clyde” and “herring in the Celtic Sea” (Division VIIa South of 52° 30′ N and VIIg,h,j) (Figure 1). The Clyde and Celtic Sea herring are not considered in this study. The population units considered in this study are named for three different ICES areas, VIaN, VIaS/VIIb,c and VIIaN and are each assumed to represent a spawning (population) unit. They separate for spawning into the areas they are named after, while during the feeding season parts (or all) of each population unit migrate to the summer feeding areas along the Hebrides/Malin Shelves where they may be susceptible to the fishery that is active within the area (see also Figure 1).

Historical dynamics

The VIaN, VIaS/VIIb,c and VIIaN population unit initialisations were taken from the ICES assessments (ICES, 2012a). Based on the estimated variance-covariance matrix in these assessments, and the use of a multivariate normal distribution, 100 different realisations of numbers-at-age and fishing mortality-at-age were generated to reflect the uncertainty in the assessments and fishery independent surveys. Catch and survey time series were truncated to the years for which the assessments were assumed to be reliable. Because each stock assessment spans different age ranges, all stocks were truncated to the lowest plus group used of the three (age 8+ winter rings). It was therefore necessary to re-estimate numbers-at-age via an update assessment (see 2.4 for assessment technique). Due to the statistical nature of stock assessments, the estimated numbers-at-age and fishing mortality-at-age deviated slightly from numbers calculated via the theoretical survival and Baranov catch equations (Appendix (A) Eqn A4, A5, A8 and A16). A correction was applied to estimated numbers fulfilling this requirement without jeopardising overall trends. To align all populations, all historical time series were truncated to start in 1970 and end in 1998.

Population unit mixing

The term mixing is used where more than one population unit is physically occurring in the same location, thus any fishery will have a likelihood of capturing more than one unit in any single haul. On a yearly basis, mixing is simulated by assuming a constant percentage of each population unit that is present in a management area other than the one it is named after. The assumptions made on the extent of mixing alter the dynamics of the three population units, not only in the future but also in retrospect. A number of mixing scenarios were assumed for each population unit resulting from different proportions of VIaS/VIIb,c and VIIaN fish being present in the VIaN area (summer feeding area). It is assumed that no fish of the Celtic Sea unit is present in the VIaN area, mainly due to the distance between these two areas. It is to be expected that there is mixing between VIaN and the stocks immediately to the south of it, however. To ensure consistency over both historical and future years in the operating model, the population numbers-at-age were reconstructed based on the mixing assumption and catches of the fisheries. Although recorded catches cannot be assumed to be without error (ICES, 2006), they are the only 'observed' source of information available. Historical population numbers-at-age ($N^{B}_{a,t,p}$, where ^{B} denotes biological/population unit, $_{a}$ age, $_{\mathrm{t}}$ year and $_{\mathrm{p}}$ population unit) were derived from estimated stock numbers-at-age ($N^{S}_{a,t,p}$), corrected for the proportion of each population unit $_{p}$ that is present in any of the other management / fishing areas $_{f}$. If part of a population unit is present in another management area, that part is no longer available to the fishery in the management area for which it is named. The part per population unit that is available to each of the three fisheries is described by the 'availability matrix' A (Eqn 1, A3, see also Eqn A1-A2):

$$N^{B}_{a,t,p} = \frac{N^{S}_{a,t,p}}{A_{a,t,p,p}} - \sum\nolimits_{f \in [1,3] \backslash p} \left(\frac{A_{a,t,f,p}}{A_{a,t,p,p}} N^{B}_{a,t,f} \right),\ for\ p \in [1,3] \quad (\textbf{Eqn 1})$$

Note that Eqn 1 can only be solved iteratively. The VIaN population unit is numbered population unit 1, the VIaS/VIIb,c population unit 2 and the VIIaN population unit 3.

If, for example, 20% of the VIIaN population unit appears in the VIaN area, and the remaining 80% is present in the VIIaN area, then the estimate of the VIIaN stock numbers-at-age is based on only 80% of the population unit catches. The availability matrix element $A_{a,t,p,p}$, where in this case $_p$ represents the VIIaN unit, would amount to 0.8, indicating that only 80% of the VIIaN unit remains in the VIIaN area available to the VIIaN fishery.

The mixing assumption enabled the redistribution of numbers-at-age in the historical part of the time series while estimated fishing mortalities at age (F) (see Eqn A4-A5 and A8) determined survival between 1970 and 1998. Numbers-at-age in the first year of the time series (1970) and recruits-at-age 1 were taken from the ICES assessments as input to reconstruct the time series.

Although Geffen *et al.* (2011) shows connectivity to be part of the population dynamics, straying and entrainment dynamics (Secor *et al*., 2009; Kerr *et al*., 2010) were not simulated in this study. Alternatively, we used fixed 'availability' proportions over time to simulate the development of mixed population units.

Operating model dynamics (from 1999 onwards)

Each year, recruits are added to the population, based on a Beverton and Holt stock to recruit function (Eqn A17, A18). It is assumed that the number of recruits produced depends on the productivity of the system, i.e. survival rates between eggs and recruits. As productivity is known to change considerably over time, the magnitudes in recruitment vary as well. Hence, specific year ranges (see Table 1) were selected which are thought to be similar to the current productivity levels. This should prevent overly optimistic or pessimistic predictions of offspring production. The stock-recruit model parameters were estimated based on the reconstructed population numbers-at-age and calculated Spawning Stock Biomass (SSB) (Eqn A19) while the residual pattern of the fit was used to generate an error structure (Eqn A18), trimmed to two standard deviations from the mean.

Within a cohort, survival from one year to the next for each of the population units depends on natural mortality and fishing mortality. Due to population unit mixing, encountered fishing mortality ($F^B_{a,t,p}$) by any of the population units might be caused by a variety of fisheries $_f$, each with different TACs and selection patterns. Encountered fishing mortality of a population unit $_p$ as a whole therefore depends on the availability ($A_{a,t,p,f}$) of each population unit to the fisheries, the $F^F_{a,t,f}$ of each of the fisheries and the catch weights-at-age of each fishery ($W^F_{a,t,f}$). Hence, the summed catch of all fisheries taken from one population unit $N^B_{a,t,p}$ spanning ages $_r$ to $_q$ (representing recruitment age to the plus group age, see equation below Eqn 2, top line) must be equal to the catch calculated from the population unit perspective (bottom line).

$$\left(\sum_{f\in[1,3]}\left(\sum_{a=r}^{q} N^B_{a,t,p}A_{a,t,p,f}\frac{F^F_{a,t,f}}{F^F_{a,t,f}+M_{a,t,p}}\left(1-e^{-F^F_{a,t,f}-M_{a,t,p}}\right)W^F_{a,t,f}\right)\right.$$

$$\left.-\sum_{a=r}^{q} N^B_{a,t,p}\frac{F^B_{a,t,p}}{F^B_{a,t,p}+M_{a,t,p}}\left(1-e^{-F^B_{a,t,p}-M_{a,t,p}}\right)\sum_{f\in[1,3]}\left(A_{a,t,p,f}\,W^F_{a,t,f}\right)\right)=0$$

$, for\ p \in [1,3]$ (**Eqn 2**)

It is assumed that the catches of the fleets are taken exactly and that fishing mortality can be calculated without error. Natural mortality, proportion mature, time of spawning, and weight-at-age are taken from the 2012 assessment results (ICES, 2012a). Von Bertalanffy growth curves were fitted to the weights-at-age data (selected year ranges, see Table 1) and based on the fit, new weights were drawn for each of the 100 Monte Carlo realisations (Eqn A13 and A14) for the entire time series. Proportion mature-at-age was sampled with replacement from historical observations (selected year ranges, see Table 1) available in the assessment input data for the entire time series as well.

2.2 The fishery

Within each of the three management areas, the simulated fishery targets the population complex during the feeding season when mixing between population units can occur. Hence, each fishery has access only to the fish present in the corresponding management area. Depending on the mixing scenario, a fishery in a specific management area could be targeting more than one (in part or full) population unit. At the same time, the other fisheries have less access to these population units. The combination of the three fisheries target 100% of each population unit in total. The catches of the fisheries ($C^F_{a,t,f}$) are defined by the Baranov catch equation (Eqn 3, A15) and depend on the available numbers-at-age ($N^B_{a,t,p}\ x\ A_{a,t,p,f}$), selection pattern, effort and catchability of the fishery ($F^F_{a,t,f}$), natural mortality ($M_{a,t,p}$) of a population unit and the catch weight-at-age ($W^F_{a,t,f}$) of each fishery.

$$C^F_{a,t,f} = \sum\nolimits_{p\in[1,3]} \left(N^B_{a,t,p} A_{a,t,p,f} \frac{F^F_{a,t,f}}{F^F_{a,t,f}+M_{a,t,p}} \left(1 - e^{-F^F_{a,t,f}-M_{a,t,p}}\right) W^F_{a,t,f} \right),\ for\ f \in [1,3]$$

(**Eqn 3**)

Note here that the fishing mortality inflicted by each fishery on the population complex is different from the fishing mortality encountered by each unit as population units can be susceptible to multiple fisheries. Landings are assumed to equal the catches as discarding is not simulated. Historical numbers-at-age in the landings are estimated by the ICES assessment (ICES, 2012a).

Von Bertalanffy growth curves were fitted to the landing weights-at-age data (selected year ranges, see Table 1) and based on the fit, new weights were drawn for each of the

100 Monte Carlo realisations (Eqn A9 and A10). Fleet selectivity for the projected period is assumed to be similar to the pattern fitted by the initialisation assessment (from here on: Malin Shelf assessment (see 2.4)), including the back calculated numbers-at-age and Malin Shelf survey (see 2.3). Error has been added to vary selectivity from year to year, and follows a log normal distribution, trimmed to two standard deviations from the mean (Eqn A6-A7).

2.3 The surveys

A fisheries independent Malin Shelf survey is simulated within the framework. The model mimics the summer acoustic survey (ages 1-8+) currently in place on the Hebrides/Malin Shelves, and targets the population complex of herring in VIaN, VIaS/VIIb,c and VIIaN (ICES, 2012c).

The samples collected and the densities measured during the Malin Shelf survey have to be split, as the three stocks in VIaN, VIaS/VIIb,c and VIIaN are managed separately. However, there are methodological difficulties in distinguishing the population origin of the samples obtained during the survey, and thus the splitting procedure has the potential to allocate any sample to the wrong population unit. The accuracy in the splitting process is described by a classification matrix ($R_{a,p,g}$) (Table 2). A correct classification of each sample to the correct population would correspond to 1 in this matrix. Results based on the WESTHER project (Hatfield *et al,* 2007) indicate maximum classification success rates to be in the order of 0.8. In addition, sample size of the survey largely determines the accuracy of the age structure. Under large sample sizes, the estimated numbers-at-age from the survey will approximate the true population unit age pattern; under small sample sizes, however, the age pattern can be severely distorted (De Oliveira *et al.*, 2006).

To model the survey indices ($I_{a,t,p}$), the proportion of survey samples (SI) that belong to population unit p needs to be calculated. All samples first identified as population p ($P_{a,t,g}$) are prone to classification error. Therefore, p ($P_{a,t,g}$) is multiplied with a classification success rate $R_{a,p,g}$. The resulting number is divided by the total number of survey samples to derive the corrected proportion of survey samples that belong to population unit p. This proportion is thereafter raised to the total observed numbers-at-age in the survey of all population units combined $\left(\sum_{g\in[1,3]} N^{B}_{a,t,g}\right)$ (Eqn 4, A20 and Eqn A20-A23) to represent the yearly survey index at age $I_{a,t,p}$.

$$I_{a,t,p} = \frac{\sum_{g\in[1,3]} R_{a,p,g} P_{a,t,g}}{SI}\left(\sum_{g\in[1,3]} N^{B}_{a,t,g}\right),\ for\ p\ \in [IM] \qquad (\textbf{Eqn 4})$$

In other words, for each survey sample $P_{a,t,g}$ it is determined to which population unit it belongs, taking classification success $R_{a,p,g}$ into account. Each survey sample represents a proportion of the entire fish abundance $\sum_{g\in[1,3]} N^{B}_{a,t,g}$ encountered during the survey. This proportion is directly related to the sample size SI. IM identifies the population units surveyed in the Malin Shelf survey.

After splitting the Malin Shelf survey samples, three indices remain that each provide information on a particular population unit. The derived VIIaN index of the Malin Shelf survey is not used in the simulations however and is replaced by a population unit specific survey (Eqn A24). This is in fact similar to the real situation since there is an acoustic survey within the Irish Sea, which targets fish at spawning time (see ICES, 2012c).

2.4 The stock assessment procedure

The perception of stock status is generated through the explicit inclusion of a stock assessment in the simulation, which is based on fishery-independent (surveys) and -dependent (landings) data. By combining population unit parameters, catches and survey indices, all information sources necessary to perform an assessment are available. The biological parameters contributing to the perception of the stock are management area specific. Hence, only population unit *x* contributes to the biological parameters of stock *x* whereas the catches of stock *x* may be a combination of individuals from different population units. Note that the (potential) mix of population units in the fisheries catch data is taken directly as input to the assessment, while survey indices are based on survey catches that are corrected to represent population unit abundances. The assessment performed uses an Integrated Catch at Age analysis (ICA) method, embedded within the FLR software, using the R platform (Patterson, 1998; Kell *et al.*, 2007; R Development Core Team, 2008; Simmonds, 2009). Within the assessment, stock numbers-at-age, as well as the harvest patterns, are estimated by minimizing the likelihood function.

In order to estimate and simulate uncertainty patterns for processes from 1999 onwards, such as survey selectivity and fisheries selection patterns, a starting condition/initialisation ICA assessment was run, which incorporated the Malin Shelf survey. The Malin Shelf survey index was split into three indices (while only the VIaN and VIaS/VIIb,c indices were used) and assigned to each of the putative stocks (population units, management areas). Note that in this case, the Malin Shelf survey indices differ with each mixing scenario while the catch matrices remain identical under all scenarios.

Von Bertalanffy growth curves were fitted to the stock weights-at-age data (selected year ranges, see Table 1) and based on the fit, new weights were drawn for each of the 100 Monte Carlo realisations (Eqn A11 and A12). Simulated weights-at-age in the landings were assumed to be similar to the weights-at-age observed in the fishery.

2.5 Management

The results from the initialisation assessments were used as starting conditions for the calculation of area specific Total Allowable Catches (TACs) (ICES, 2012a). The assessed stocks were projected forward two years in time, assuming constant recruitment (geometric mean of recruitment over the most recent five years) and weights-at-age equal to the moving average over two years. Catches one year ahead are set to the proposed TAC for the intermediate year as obtained from the projections the year before. TACs for the advisory year were calculated on the basis of F_{MSY} targets in the case of the VIaS/VIIb,c and VIIaN stocks (ICES, 2012a) and according to the management plan for the VIaN stock (Council Regulation (EC) No 1300/2008) (Eqn A26). A modification to the VIaN management plan had to be made to eliminate the option of zero catches in case SSB dropped below 50 000 tonnes, as such conditions could not be evaluated within the ICA assessment due to technical constraints. Under those circumstances, the TAC would be calculated on the basis of a 0.05 fishing mortality per year. F_{MSY} values were not estimated within the simulation framework but directly taken from ICES (2012a) as the same ICES assessment data were used as starting conditions for the simulations in this study and the estimation of F_{MSY} by ICES. In 1999, at the transition from the historical to the simulated period, no TACs were imposed. Hence, in this situation for the intermediate year a management target equal to the management target for the advisory year was used.

The fisheries were expected to fully utilise the TACs, and hence fishing mortality can be calculated based on the number of fish available to the fishery. The projected mortality by each fishery was implemented the year after and results in a population unit catch and fishing mortality. This scheme enabled a full-feedback analysis of the management strategy evaluation.

2.6 Scenario descriptions

In total, three different processes are varied to study their effects on management of the stock: classification success, the extent of mixing and the sample sizes from the fishery independent survey. In each case, the Malin Shelf survey is only used to manage the VIaN and VIaS/VIIb,c stocks and not the VIIaN stock.

1. Mixing scenario: with mixing proportions according to Table 3. The mixing proportion is not known, hence, assumptions have to be made to what extent VIaS/VIIb,c, VIaN and VIIaN fish mix during the feeding season. As low mixing proportions already have major implications, values of 20%, 10%, 5% mixing and no mixing were simulated. Sample size from the fishery independent survey equals 1500 y^{-1}. Classification success is assumed to be 1 (100%) for each population unit.
2. Classification scenario: with varying accuracy of correctly classifying samples of the population units in the Malin Shelf survey ranging between 0.7 and 1 correct in steps of 0.1 (70% - 100% in steps of 10%). No mixing is assumed to occur.
3. Sample size scenario: with varying numbers of samples taken for classification and age composition in the Malin Shelf survey ranging between 750 and 6000 samples/individuals (three-fold change in sample size). The 1500 individuals as a sample size is approximately the number currently taken in the synoptic acoustic Malin Shelf survey executed since 2008. Classification success is assumed to be 1 for each population unit.
4. Base scenario: Evaluating the most likely settings based on expert knowledge with varying mixing proportions according to Table 3, combined with a sample size of 1500 individuals y^{-1} on board the Malin Shelf survey. Classification success was set to 0.8 for each population unit, as taken from WESTHER project findings (Hatfield *et al.*, 2007). Assessment results in the initialisation phase (data up to 1998) of this scenario are used to extract weighted residuals from the assessment survey fits. Since all base scenarios, with varying mixing proportions, are

evaluated with identical catch-at-age matrices (as given by ICES assessments (ICES, 2012a)), the sum of the weighted survey index residuals (the simulated Malin Shelf survey), is taken as a measure of the likelihood of each base scenario. The most likely mixing proportion is described by the base scenario with the lowest sum of weighted residuals. For this analysis, the range of mixing scenarios has been extended with mixing proportions up to 25% and 30%.

For each scenario, the catch composition and survey indices used for the stock assessment are specified in Table 4.

3. Results

3.1 Effects of mixing scenarios

No substantial change in the Stock Recruitment Relationship (SRR) occurred among mixing scenarios, when fitted to the assessed stock data (see Figure 2, dotted lines, note herein that the survey index is mixing scenario specific but the catch matrix is identical). In contrast, the ‘true’ relationship between recruitment and SSB obtained from fitting a recruitment curve to the population units reveals that the productivity of VIaN is considerably higher (more recruits per spawner) while the productivity of VIaS/VIIb,c and VIIaN is lower than estimated based on assessed stock data, at high mixing proportions. This result is to be expected as the stock assessment of VIaN overestimates total population size (at high mixing proportions), due to its larger catch which originates from all three population units, thereby underestimating the number of recruits per spawner. The reverse is true for the other two population units.

The effect of population unit mixing on stock management is evaluated while other processes, such as fish classification on board surveys or exploitation level, are kept relatively constant. Figure 3 gives an overview of the four different mixing scenarios and the development of SSB in the stocks, divided by the ‘true’ development in SSB in each of the population units. These plots show that whenever there is no mixing between population units (0% column), each stock’s SSB development is estimated to be nearly identical to the true population unit SSB and is hence positioned on top of the y=1 line. When mixing proportions increase however (column 5% to 20%), the divergence between the stocks and the population units increases. Note, however, that due to a slight difference in simulated maturity between the VIaN stock and population unit, the SSB ratio is positioned just above y = 1. The noise in the period before 1999 is due to the limited variability in catch-at-age over all 100 realisations and highly variable fishing mortalities over time.

The VIaN stock is estimated to be increasingly inflated relative to the VIaN population unit with increasing mixing proportions (see Figure 3, above y=1). This increase is mainly driven by larger numbers in the catch-at-age matrix as the catch of the simulated VIaN fishery comprises a mixture of VIaN, VIaS/VIIb,c and VIIaN fish rather than VIaN fish alone. Besides absolute catch, cohort patterns play an important role in stock assessments. All three population units present in the VIaN catch follow more or less the same decay as all are fished with similar fishing mortalities. Therefore the catch composition-at-age does not contrast markedly to the survey index age composition, which is based on the VIaN population unit only. Hence, the assessment F and true population unit F estimates are similar. The opposite is true for the VIaS/VIIb,c and VIIaN stocks that are estimated to be smaller than the actual population size. What is unexpected is the near to perfect estimation of the VIaS/VIIb,c SSB of the stock versus the population unit; an underestimation would be expected. This can be explained by two processes. Firstly, the part of the VIaS/VIIb,c population unit that is caught in the VIaN area is fished at a lower F than the remaining part in the VIaS/VIIb,c area. Therefore, the majority (more than what would be expected based on the mixing scenario) of the catch of the VIaS/VIIb,c population unit is taken inside the VIaS/VIIb,c area. Hence, catch and population unit decay match up well. Secondly, the survey indicates that the survival of fish is higher than what could be expected based on the catches only, due to a somewhat lower fishing mortality encountered in the VIaN area. This causes the stock assessment to overestimate biomass of older fish and underestimate biomass of younger fish, thereby increasing the estimate of SSB in the stock and becoming more similar to the true population unit SSB. The small bump early in the VIaS/VIIb,c time series is caused by an estimation difference in the plus group at times when the VIaS/VIIb,c population unit was at its time series low and small deviations make up for a large relative difference.

3.2 Effects of classification problems

The results indicate that, apart from the SSB deviations already discussed under 3.1, classification uncertainty has only a minor effect on SSB estimation (Figure 4) (as well as F and recruitment, not shown). This is because the VIaN and VIaS/VIIb,c population unit abundances are of similar size. Therefore misclassification has less of an effect because the total number of misclassified fish is equal in both directions and the displacement of misclassified fish from one index to the other index equals out. Also note that the VIIaN survey index is not based upon the Malin Shelf survey and hence is not affected by the misclassification problem. If population unit abundances were different to a larger extent, such as is the case for VIIaN, which is c. 10-fold less abundant relative to either VIaN or VIaS/VIIb,c, the misclassification would severely distort the age composition.

3.3 Effects of sample size in the Malin Shelf survey

Since the number of survey samples taken from one population unit is proportional to the abundance of that population unit; lower numbers of samples are taken from the smaller population units. This sampling procedure has the greatest effect on the index of the smallest population unit being surveyed, in this case the VIIaN unit, as few samples are available to derive an age composition for this unit.

Under each of the four sample size scenarios evaluated, no clear effect of sample size in the survey could be detected. If the age composition was to be severely distorted, it could be expected that the assessment indicates stock development in a different direction than the population unit SSB. The expected result is not visible, however, with any of the sample sizes used here, nor is there any advantage of doubling or quadrupling the sample size. Again this is because the VIaN and VIaS/VIIb,c population unit abundances are of similar size, harvested with fishing mortalities in the same order of magnitude, and similar productivity occurs for the two population units. For these reasons, the age composition and abundance of each of these population units is comparable and equally available to the survey. In the case of the VIIaN index, however, the age composition was highly skewed in the Malin Shelf survey. On average, only 1 out of 20 individuals would be assigned to the VIIaN survey index, as abundance of the VIaN and VIaS/VIIb,c population units are on average ten times larger. This implies that the majority of adult age classes in the survey index (e.g. ages 4:8) of the VIIaN stock are made up on the basis of approximately ten fish.

3.4 Base scenario

The results indicate that for all three stocks, the 20% mixing scenario is associated with the lowest sum of weighted residuals (Figure 5). The lowest sum of weighted residuals can be used here as an appropriate indicator of the likely mixing scenario as sample size and classification success do not show a marked effect on abundance estimation. The 20% mixing scenario is therefore assumed to represent, given the scenarios tested, the most likely situation in the population complex, i.e. the most likely scenario.

Furthermore we contrast the development in SSB, which is partly a result of management but is also linked to the productivity of the population unit itself, against the limit reference points set by ICES (2012a) (see Figure 6). Where the lower 5th percentile of the SSB series extends below the limit biomass line, there is an increased risk of impaired recruitment, a situation management wants to avoid. Increased mixing of population units, and not being able to account for mixed catches, shows an increased risk to sustainable management of the VIaN stock as stock size is overestimated in the assessment. This overestimation results in higher quota which translates into higher fishing mortalities as well. Management of the VIaS/VIIb,c stock, however, only approaches sustainable levels under the 20% mixing scenario and is highly unsustainably managed under all other mixing proportions. The comparison against limit reference points defined by ICES may be questionable in this context as the reference points have been estimated outside the model. In any case, however, underestimating the proportion of mixing does not pose problems for the VIaS/VIIb,c stock as SSB series rise with increasing mixing proportions. The same conclusions apply to the VIIaN stock, stressing though that the stock is sustainably managed under all scenarios especially as the simulated productivity is high resulting in a sharp increase in SSB. The additional effects of sample size and classification success on sustainable management are small (additional risk between 0% and 2%).

4. Discussion

4.1 Management implications related to population unit mixing

Population units that mix during (part of) the fishing season pose several different problems for management. First of all, assessing stock status on the basis of a mixture of population units in the catch is the main driver of biased estimates of true abundances, a conclusion also supported by Guan *et al.*(2013). It is, therefore, of utmost importance to be able to allocate individuals in mixed catches to the population unit to which they belong. To highlight the importance of correct allocation, we assumed in this study that catches from the VIaN fisheries were taken from mixed aggregations and that no effort is undertaken to allocate catches to their 'true' population unit. Due to the lack of accurate reallocation in our simulations, biomass levels were estimated with great bias. This is a common problem. Effort has been spent to reduce the potential bias in the assessment in, for example, the North Sea and Skagerrak/Kattegat (ICES area IIIa) herring assessments (Clausen *et al.*, 2007) , the North Sea plaice (*Pleuronectes platessa*) assessment (Ulrich *et al.*, 2013) and also here in the simulated Malin Shelf survey, indicating that methods and simulation tools are available. In reality, perfect allocation will likely not exist (evaluated in this study as a low mixing proportion scenario) and the lack of it could already jeopardise sustainable management. The simulation results by Guan *et al.* (2013) show a very similar bias for both SSB and F under their spatially structured population, fisheries and management scenario (PF-M). This scenario is most similar to our framework design. Guan *et al.* (2013) demonstrate that SSB tends to be overestimated and F underestimated in areas where fish aggregate during the fishing season, similar to the bias in the VIaN management area.

In addition, the estimated productivity of each of the population units, defined as recruit per spawner, was also shown to be biased, due to lack of accurate reallocation, an element also brought forward by Frank and Brickman (2000) and Kell *et al.* (2009). Productivity of populations plays an important role in defining management targets such as F_{MSY} or biomass reference levels. Due to the lack of knowledge on mixing proportions or tools to correct for it, adopting MSY targets based on biased productivity estimates can result in substantial over-exploitation. Accurate biomass reference levels are important to ensure that SSB is kept above a threshold to reduce the risk of impaired recruitment (FAO, 1996). Hence, inferences made with respect to biomass reference points and recruitment driven MSY estimates should be treated with care under these circumstances (Bartley *et al.*, 1996).

4.2 Added value of fisheries independent surveys

We show that fisheries independent data can counter, only to a small extent, the bias in stock assessments where a mixture of population units occur in the fisheries catches. This is caused mostly by the design of assessment models such as ICA (Patterson, 1998; Simmonds, 2009), which has been used in this study, or XSA (Shepherd, 1999) where catch-at-age data are fitted with only small error margins by default. Because of this, assessment results are likely to follow patterns observed in the catch, even when fisheries independent data indicate otherwise. In those cases where it was expected that reliable catch data were not available, fisheries independent assessment models have been designed and used (Beare *et al.*, 2005; Mesnil *et al.*, 2009). It is, however, in retrospect, difficult to argue that catch data contain larger errors or bias compared to survey data, especially when data to support such a conclusion are lacking. Assessment models that independently weight survey indices according to internal consistency and noise (ICES, 2012a; ICES, 2012b), or allow prior weighting for surveys (Hollowed *et al.*, 2000) should be used instead. Another option is to perform a coherent assessment of the full population complex, modelling unit mixing and mixed removals by different fleets as performed by Cunningham *et al.* (2007) or Heath *et al.* (2008) or by modelling a simplified ‘lumping of population units’ version by Kell *et al.* (2009). However, one can question if this will lead towards simpler and more precautionary fisheries management (Reiss *et al.*, 2009) since an increase in complexity also requires more data to parameterise these models.

In cases where area mixing and spawning origin classification issues play a role, it is necessary to invest additional effort into monitoring the smaller population units in the population complex, as these are most vulnerable. The proportion of fish from the smaller population unit encountered in a combined survey will be low, which makes it difficult to derive a reliable age distribution. In this study, the design of the Malin Shelf survey contributes to this aspect, in that it is assumed to be a fully random survey with equal encounter rates for each of the population units at the survey stations. In combination with classification error, the smaller population unit survey index becomes a reflection of the larger unit densities rather than a poorly sampled composition of the population unit itself. Managing on such a basis might pose problems if the development of individual population units are not in synchrony, which could lead to over-exploitation, the loss of spawning units and therefore also resilience of the population complex (Holling, 1973; Begg *et al.*, 1999; Scheffer *et al.*, 2001; Smedbol and Stephenson, 2001). Investing the additional effort is especially important when one doubts the quality of the catch data. Being able to contrast the catch data with a reliably estimated age composition from another data source, such as a survey, might prevent users from putting too much confidence into the ability of catch data driven assessments to reflect reality.

Classification of fish catch to their spawning origin is specifically important to improve the quality of fishery and survey catch data. Being able to create catch-at-age matrices for both data sources without bias could well be the solution for complex population management. Accurate classification requires substantial sampling and potentially the use of a suite of techniques (Campbell *et al.*, 2007; Hatfield *et al.*, 2007; Bierman *et al.*, 2010; Geffen *et al.*, 2011). Although these techniques might not be able to provide 100% classification success, management plans can and should be designed in such a way that this element of uncertainty is taken into account (Stephenson, 1999; Cunningham *et al.*, 2007; Reiss *et al.*, 2009). Misclassification in the simulations assumed that there is an equal chance that fish are assigned to each of the other two population units and the proportion misclassified is equal in each population unit. In reality, when survey samples are split (using e.g. otolith and / or body morphometrics techniques) misclassification might not be so symmetrical. Due to asymmetry, the displacement of misclassified fish from one index to the other index might be uneven, even when the VIaN and VIaS/VIIb,c population units are similar in size.

4.3 Likely mixing proportion

Assuming a fixed mixing proportion, this study shows that, on the basis of a historical back-calculation of numbers-at-age in each of the simulated population units, a mixing proportion of approximately 20% is most likely for the period up until 1998. It should be noted, however, that the 15% and 10% scenarios show similar results and that variable mixing proportions over time or mixing in either the VIaS/VIIb,c or VIIaN areas were not tested. One of the core assumptions in this estimation is that the unit stock is well defined under each of the tested scenarios, not violating the assumptions of a stock assessment itself (Hart and Cadrin, 2004). Comparing the scenarios on a statistical basis poses problems, as the underlying survey data (not the catch data) changes from scenario to scenario. If, however, catch-at-age and survey data at-age are in agreement, this should result in lower overall residuals in an assessment, which forms the basis of our conclusion. Due to the lack of empirical data to support any hypothesis on mixing, modelling is the only tool that can be used to estimate historical mixing proportions. Modelling these likely proportions though, together with historically observed survey sample size and classification success in one framework, does provide us here with more realistic information on the ability to manage the population units sustainably.

4.4 Mismatch between population unit and stock

One could question whether a 20% mixing proportion classifies as a mismatch between biological and management spatial scales, as pointed out to be an important aspect of complex population management (Iles and Sinclair, 1982; Stephenson, 1999; Frank and Brickman, 2000; Reiss *et al.*, 2009; Cope and Punt, 2011; Ulrich *et al.*, 2013). The population units considered here only mix during the summer months, when they migrate across the shelf to forage. Historically, the fishery in VIaN was active during this period and likely caught a mixture of population units. At spawning time they can be treated as separate units, spatially appropriately defined by the management area boundaries. In essence, there seems to be no mismatch between biological and management scale there. It is only that a large portion of the catch used to be taken during the summer months, by a fishery limited by quota based on sustainable fishing mortalities. If these sustainable fishing mortalities differ greatly between population units, managing according to the most vulnerable unit will be a sustainable solution for the entire population complex (Reiss *et al.*, 2009). This will, however, automatically result in the under exploitation of other population units in the complex. More recently the fisheries on the population complex have been organised outside the population unit mixing season and area, and the fisheries independent survey index therefore is the only data source that is prone to bias introduced by mixing population units. In combination with the results discussed above, this could mean that recent estimates of abundance based on stock assessment models are less biased than is estimated for the period prior to 1998. To perform time series analyses of individual population units is therefore advisable, hereby taking the shift from a historical mixed to a more recent non-mixed catch into account.

4.5 Conclusion

Sustainably managing a complex population structure can be very challenging and simulation studies are essential to improve our knowledge of fish and fisheries behaviour (Kerr *et al.*, 2010). This study and others stress the importance of carefully scrutinising for a mismatch between biology and management (Andrews *et al.*, 2006). If one doubts whether catch data are of good enough quality for stock assessment because of potential population unit mixing in the catches, a well-designed survey could provide an additional dataset to contrast the fisheries catch information. However, the ability of the survey to limit the bias in the assessment results should be investigated before implementation.

High success rates in classification of fish are necessary with all data collection programs and should improve the accuracy of catch-at-age data, the cornerstone of providing precautionary management advice. With the help of Management Strategy Evaluation, the effects of errors in classification and uncertainty regarding mixing proportion can be investigated and could result in operational management plans that take these aspects into account.

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Figure captions

Figure 1: Overview of study area. The shaded areas represent the main spawning locations of the population units in VIaN, VIaS/VIIb,c and VIIaN (spawning grounds for the areas under consideration only). The management areas are defined by the black solid lines while the arrows illustrate the migration routes of the population units towards the summer feeding areas along the Hebrides and Malin shelves' edge.

Figure 2: Fitted stock-recruitment relationship (SRR) for all three stocks / population units (VIaN, VIaS/VIIb,c and VIIaN) under four mixing scenarios (0% - 20%). The horizontal axis represents SSB (thousand tonnes) while the vertical axis represents number of recruits (in millions). The dotted lines reflect the median SRRs estimates out of 100 Monte Carlo simulations, based on the assessed stock dynamics while the solid coloured lines represent the SRRs based on the 'true' population unit dynamics of the operating model.

Figure 3: Time series of estimated stock SSB divided by true population unit SSB for all three stocks / population units (VIaN, VIaS/VIIb,c and VIIaN) under four mixing scenarios (0% - 20%). The horizontal axis represents the years of the simulation while the vertical axis represents the ratio between stock SSB and true population unit SSB. A ratio of one (y=1) represents full agreement between stock assessment and population unit SSB. 95% confidence intervals are given in coloured dashed lines. 95% CIs are calculated on the basis of 100 Monte Carlo simulation results.

Figure 4: Time series of estimated stock SSB divided by true population unit SSB for all three stocks / population units (VIaN, VIaS/VIIb,c and VIIaN) under four classification success rates (1 – 0.7). The horizontal axis represents the years of the simulation while the vertical axis represents the ratio between stock SSB and true population unit SSB. A ratio of one (y=1) represents full agreement between stock assessment and population unit SSB.95% confidence intervals are given in coloured dashed lines. 95% CIs are calculated on the basis of 100 Monte Carlo simulation results.

Figure 5: Sum of weighted survey residuals in the assessments of VIaN (left), VIaS/VIIb,c (middle) and VIIaN (right) spanning 1970-1998. The horizontal axis represents the mixing proportion increasing from high mixing proportions (30%) to no mixing at all (0%). The vertical axis represents a qualitative scale of the sum of weighted survey residuals. The first and third quartile of each dataset are represented by the shaded boxes, while minimum and maximum observations, not being outliers, are represented by the dotted vertical lines. Quartiles are calculated on the basis of 100 Monte Carlo simulation results.

Figure 6: Time series of all three population unit SSB (VIaN, VIaS/VIIb,c and VIIaN) under four mixing scenarios (0% - 20%). The horizontal axis represents the years of the simulation while the vertical axis represents true population unit SSB. The thick dashed horizontal lines indicate the biomass limit reference points (B_{lim}) for each of the stocks. 95% confidence intervals are given in coloured dashed lines. 95% CIs are calculated on the basis of 100 Monte Carlo simulation results.

Table captions

Table 1: Selected year classes produced during productivity levels thought to be similar to current levels and used to reconstruct population numbers-at-age and calculate SSB. Proportion mature time series were selected for the entire historical time series while weight-at-age time series were selected to represent expected growth rates given the selected productivity levels.

Table 2: Classification matrix. Values on the diagonal indicate the proportion of samples that is correctly classified (in this case 0.8). All other values indicate the proportion of incorrectly classified samples and which are allocated to another population unit.

Table 3. Availability of populations to fisheries under different population mixing regimes expressed as percentages of the total population. Same percentages apply across all ages and all years.

Table 4: Origin of assessment catch and survey data for each of the scenarios evaluated. Malin Shelf split refers to the calculation method used to split the synoptic Malin Shelf survey, covering the VIaN, VIaS/VIIb,c and VIIaN population units during one survey, into individual population unit indices.

Table 1: Selected year classes produced during productivity levels thought to be similar to current levels and used to reconstruct population numbers-at-age and calculate SSB. Proportion mature time series were selected for the entire historic time series while weight-at-age time series were selected to represent expected growth rates given the selected productivity levels.

Population unit / stock	*Productivity*
	year-classes
VIaN	1989-2006
VIaS/VIIb,c	1970-1980,1986-1998
VIIaN	1963-2005
	Growth data
	years
VIaN	1991-2005
VIaS/VIIb,c	1991-2005
VIIaN	1989-2005
	Proportion mature
	years
VIaN	1970-1998
VIaS/VIIb,c	1970-1998
VIIaN	1970-1998

Table 2: Classification matrix. Values on the diagonal indicate the proportion of samples that is correctly classified (in this case 0.8). All other values indicate the proportion of incorrectly classified samples and which are allocated to another spawning component.

			Allocation	
	Population unit	**VIaN**	**VIaS/VIIb,c**	**VIIaN**
Origin	**VIaN**	0.8	0.1	0.1
	VIaS/VIIb,c	0.1	0.8	0.1
	VIIaN	0.1	0.1	0.8

Table 3. Availability of populations to fisheries under different population mixing regimes expressed as percentages of the total population. Same percentages apply across all ages and all years.

		VIaN Fishery	
Mixing scenario	*VIaN Population unit*	*VIaS/VIIb,c Population unit*	*VIIaN Population unit*
20%	100	20	20
10%	100	10	10
5%	100	5	5
0%	100	0	0
		VIaS/VIIb,c Fishery	
20%	0	80	0
10%	0	90	0
5%	0	95	0
0%	0	100	0
		VIIaN Fishery	
20%	0	0	80
10%	0	0	90
5%	0	0	95
0%	0	0	100

Table 4: Origin of assessment catch and survey data for each of the scenarios evaluated. Malin Shelf split refers to the calculation method used to split the synoptic Malin Shelf survey, covering the VIaN, VIaS/VIIb,c and VIIaN population units during one survey, into individual population unit indices.

Scenario	Stock	Catch	Survey
Mixing	VIaN	Mixture of VIaN, VIaS/VIIb,c and VIIaN fish	Malin Shelf split
	VIaS/VIIb,c	VIas/VIIb,c fish only*	Malin Shelf split
	VIIaN	VIIaN fish only*	VIIaN acoustic
Classification	VIaN	VIaN fish only	Malin Shelf split
	VIaS/VIIb,c	VIaS/VIIb,c fish only	Malin Shelf split
	VIIaN	VIIaN fish only	VIIaN acoustic
Sample size	VIaN	VIaN fish only	Malin Shelf split
	VIaS/VIIb,c	VIaS/VIIb,c fish only	Malin Shelf split
	VIIaN	VIIaN fish only	VIIaN acoustic
Base	VIaN	Mixture of VIaN, VIaS/VIIb,c and VIIaN fish	Malin Shelf split
	VIaS/VIIb,c	VIas/VIIb,c fish only*	Malin Shelf split
	VIIaN	VIIaN fish only*	VIIaN acoustic

* Only a proportion of the total population unit is present in the area (depending on mixing scenario)

Equations

Historic population dynamics

Stock numbers at age, time and area $N^S_{a,t,f}$ are back-calculated based on the 'true' population numbers $N^B_{a,t,p}$ (as assumed by the mixing scenario) by multiplying $N^B_{a,t,p}$ with the availability / spatio-temporal presence of a population in a certain area $A_{a,t,p,f}$ and summing over population units $_p$.

(Eqn A1) $N^S_{a,t,f} = \sum_{p\in[1,3]}\left(N^B_{a,t,p}A_{a,t,p,f}\right),\ for\ f \in [1,3]$

Summed numbers by area at age and time are identical to summed numbers by population unit at age and time.

(Eqn A2) $\sum_{f\in[1,3]} N^S_{a,t,f} = \sum_{p\in[1,3]} N^B_{a,t,p}$

A rewrite of Eqn 1 to bring $N^B_{a,t,p}$ to the left-hand side results in Eqn 3.

(Eqn A3) $N^B_{a,t,p} = \frac{N^S_{a,t,p}}{A_{a,t,p,p}} - \sum_{\substack{f\in[1,3]\\ f\neq p}}\left(\frac{A_{a,t,f,p}}{A_{a,t,p,p}}N^B_{a,t,f}\right),\ for\ p \in [1,3]$

Population dynamics

Survival of population unit $_p$ numbers at age to year $_{t+1}$ follows from numbers at age in year $_t$ and total mortality (of the true population unit) $Z^B_{a,t,p}$.

(Eqn A4) $N^B_{a+1,t+1,p} = N^B_{a,t,p}e^{-Z^B_{a,t,p}},\ for\ p \in [1,3]$

Survival of fish to year $_{t+1}$ that enter or are present in the plus group $_q$ (age bin in which all ages at the age of $_q$ or higher are combined) follows from the numbers at the last true age $_{q\text{-}1}$ and total mortality at the last true age, plus the numbers already present in the plus group.

(Eqn A5) $N^B_{q,t+1,p} = N^B_{q-1,t,p}e^{-Z^B_{q-1,t,p}} + N^B_{q,t,p}e^{-Z^B_{q,t,p}},\ for\ p \in [1,3]$

Mortality rates

The fishing mortality that is imposed by fishery $_f$ ($F^F_{a,t,f}$) is calculated on the basis of the selection pattern of the fleet $Sel^F_{a,\bar{t},f}$, the error pattern therein $\varepsilon^F_{a,t,f}$, the effort of the fleet $E_{\bar{t},f}$and the catchability of the fleet $Q_{\bar{t},f}$.

(Eqn A6) $F^F_{a,t,f} = \left(Sel^F_{a,\bar{t},f}\varepsilon^F_{a,t,f}\right)E_{\bar{t},f}Q_{\bar{t},f},\ \ for\ f \in [1,3]$

(Eqn A7) $\varepsilon^F_{a,t,f} \sim lnN(0,\left(\sigma^{Sel}_{a.f}\right)^2)$

Total mortality encountered by a population unit $Z^B_{a,t,p}$ is given as the sum of the encountered fishing mortality and the natural mortality of the population unit.

(Eqn A8) $Z^B_{a,t,p} = F^B_{a,t,p} + M_{a,t,p},\ \ for\ p \in [1,3]$

Weights at age

Weight at age in the fishery $W^{F}_{a,t,f}$, in the stock $W^{S}_{a,t,f}$ and in the population unit $W^{B}_{a,t,p}$ is modelled following the von Bertalanffy growth equation specifying weight at infinity $Winf^{F}_{f}$, a curvature parameter K^{F}_{f}, a fish' length at birth $t0^{F}_{f}$ and length-weight relationship parameters *a* and *b* and a fleet, stock, population unit specific error term $\varepsilon^{W}_{a,t,f}$.

(Eqn A9) $W^{F}_{a,t,f} = Winf^{F}_{f}(1 - e^{-K^{F}_{f}\left(a - t0^{F}_{f}\right)})^{b} + \varepsilon^{WF}_{a,t,f},\ for\ f \in [1,3]$

(Eqn A10) $\varepsilon^{WF}_{a,t,f} \sim lnN(\overline{W^{F}_{a,f}}, \left(\sigma^{WF}_{a,f}\right)^{2})$

(Eqn A11) $W^{S}_{a,t,f} = Winf^{S}_{f}(1 - e^{-K^{S}_{f}\left(a - t0^{S}_{f}\right)})^{b} + \varepsilon^{WS}_{a,t,f},\ for\ f \in [1,3]$

(Eqn A12) $\varepsilon^{WS}_{a,t,f} \sim lnN(\overline{W^{S}_{a,f}}, \left(\sigma^{WS}_{a,f}\right)^{2})$

(Eqn A13) $W^{B}_{a,t,p} = Winf^{B}_{p}(1 - e^{-K^{B}_{p}(a - t0^{B}_{p})})^{b} + \varepsilon^{WB}_{a,t,p},\ for\ p \in [1,3]$

(Eqn A14) $\varepsilon^{WB}_{a,t,p} \sim lnN(\overline{W^{B}_{a,p}}, \left(\sigma^{WB}_{a,p}\right)^{2})$

Catch equation

The catch of a fishery $C^{F}_{a,t,f}$ is modelled following a modification of the Baranov catch equation. Here, the population numbers are determined by the availability of population units to a fishery $N^{B}_{a,t,p}A_{a,t,p,f}$, the fraction of total mortality caused by fishing $\frac{F^{F}_{a,t,f}}{F^{F}_{a,t,f}+M_{a,t,p}}$ and the decay in population numbers due to mortality $1 - e^{-F^{F}_{a,t,f}-M_{a,t,p}}$.

(Eqn A15) $C^{F}_{a,t,f} = \sum_{p\in[1,3]}\left(N^{B}_{a,t,p}A_{a,t,p,f}\frac{F^{F}_{a,t,f}}{F^{F}_{a,t,f}+M_{a,t,p}}\left(1 - e^{-F^{F}_{a,t,f}-M_{a,t,p}}\right)\right),\ for\ f \in [1,3]$

The amount of fish caught (in kg) from a population unit $C^{B}_{a,t,p}$ depends on the population unit numbers times the fraction of the total mortality caused by all fisheries and the decay of a population unit due to all mortality causes.

(Eqn A16) $C^{B}_{a,t,p} = N^{B}_{a,t,p}\frac{F^{B}_{a,t,p}}{F^{B}_{a,t,p}+M_{a,t,p}}\left(1 - e^{-F^{B}_{a,t,p}-M_{a,t,p}}\right),\ for\ p \in [1,3]$

Stock-recruitment relationship (Beverton and Holt)

Recruits at age r are added to a population unit following a Beverton & Holt stock to recruit relationship with parameters $\propto_{p}$ and β_{p}, Spawning Stock Biomass $SSB_{t,p}$ and an error term $\varepsilon^{SRR}_{t,p}$.

(Eqn A17) $N^{B}_{r,t,p} = \frac{\propto_{p} SSB_{t-1,p}}{\beta_{p}+SSB_{t-1,p}}\varepsilon^{SRR}_{t,p},\ for\ p \in [1,3]$

(Eqn A18) $\varepsilon_{t,p}^{SRR} \sim lnN(0, {\sigma^{SRR}}^{2}_{p})$

Spawning Stock Biomass

Spawning stock biomass is calculated as the sum over all ages for numbers at age $N_{a,t,p}^{B}$ multiplied with weight at age $W_{a,t,p}^{B}$ and maturity at age $O_{a,t,p}^{B}$.

(Eqn A19) $SSB_{a,t,p}^{B} = \sum_{a=r}^{q} N_{a,t,p}^{B}\, W_{a,t,p}^{B} O_{a,t,p}^{B}$

Survey indices

To model the survey indices ($I_{a,t,p}$), the proportion of survey samples (SI) that belong to population unit p need to be calculated. All samples at first identified as population p ($P_{a,t,g}$) are prone to classification error. Therefore, p ($P_{a,t,g}$) is multiplied with a classification success rate $R_{a,p,g}$. The resulting number is divided by the total number of survey samples to derive the corrected proportion of survey samples that belong to population unit p. This proportion is thereafter raised to the total observed numbers-at-age in the survey of all population units combined ($\sum_{g\in[1,3]} N_{a,t,g}^{B}$) (Eqn 4, A20 and Eqn A20-A23) to represent the yearly survey index at age $I_{a,t,p}$.

(Eqn A20) $I_{a,t,p} = \frac{\sum_{g\in[1,3]} R_{a,p,g} P_{a,t,g}}{SI}\left(\sum_{g\in[1,3]} N_{a,t,g}^{B}\right),\ for\, p\ \in [IM]$

The number of samples $P_{a,t,p}$ that belong to population unit $_{p}$ is given by the number of times Δ_j equals to one.

(Eqn A21) $P_{a,t,p} = \sum_{j=1}^{SI}(\Delta_j),\ \ for\, p\ \in [IM]$

In total, SI times a sample is taken. The population unit and age of an individual sample is determined by drawing random numbers $S_{j,t}$ inside the range $\sum_{i=r}^{a}\sum_{g\in[1,3]}^{p} Sel_{i,t,p}^{I} N_{i,t,p}^{B}$ to $\sum_{i=r}^{a+1}\sum_{g\in[1,3]}^{f} Sel_{i,t,f}^{I} N_{i,t,f}^{B}$. Each population unit and age combination is represented by a bin width. If a random value drawn falls within the bin width, it is counted as a sample of the respective population unit and age. Bin width is determined on the basis of population unit numbers at age $N_{i,t,p}^{B}$ and selection of the survey at age $Sel_{i,t,p}^{I}$.

(Eqn A22) $\Delta_j = \begin{cases} 1\ if \left(\sum_{i=r}^{a}\sum_{g\in[1,3]}^{p} Sel_{i,t,p}^{I} N_{i,t,p}^{B}\right) \leq S_{j,t} < \left(\sum_{i=r}^{a+1}\sum_{g\in[1,3]}^{f} Sel_{i,t,f}^{I} N_{i,t,f}^{B}\right) \\ 0\ if\ \left(\sum_{i=r}^{a}\sum_{g\in[1,3]}^{p} Sel_{i,t,p}^{I} N_{i,t,p}^{B}\right) > S_{j,t} \geq \left(\sum_{i=r}^{a+1}\sum_{g\in[1,3]}^{p} Sel_{i,t,p}^{I} N_{i,t,p}^{B}\right) \end{cases}$

$, for\ j\ \in [SI]$

(Eqn A23) $S_{j,t} \sim U(0, \sum_{a=r}^{q}\sum_{p\in[IM]} Sel_{a,t,p}^{I} N_{a,t,p}^{B}),\ for\ j \in [1, SI]$

For a selection of population units, Eqn 20 is not used to derive the survey index values at age. Instead, Eqn 24 is used. Index value at age per population unit $I_{a,t,p}$ is calculated by multiplying survey selection $Sel_{a,t,p}^{I}$ with population unit abundance $N_{a,t,p}^{B}$ and an error term $\varepsilon_{a,p}^{I}$.

(Eqn A24) $I_{a,t,p} = Sel_{a,t,p}^{I} N_{a,t,p}^{B} \varepsilon_{a,p}^{I},\ for\ p\ [1,3] - [IM]$

(Eqn A25) $\varepsilon_{a,p}^{I} \sim lnN(0, {\sigma^{I}}_{a,p}^{2})$

TAC scenario

The TAC of a fishery $T_{t,f}$ is set on the basis of stock assessment results. These results specify stock numbers at age $N_{a,t,f}^{S}$ and an area specific selection pattern $Sel_{a,t,f}^{A}$. The target fishing mortality, as set by management plans or MSY objectives is given by $Ftarget$. Eqn 26 follows the Baranov catch equation.

(Eqn A26) $T_{t,f} = \sum_{a=r}^{q} N_{a,t,f}^{S}\, W_{a,t,f}^{S} \frac{Ftarget_{t,f} \cdot Sel_{a,t,f}^{A}}{M_{a,t,p} + Ftarget_{t,f} \cdot Sel_{a,t,f}^{A}} \left(1 - e^{-\left(M_{a,t,p} + Ftarget_{t,f} \cdot Sel_{a,t,f}^{A}\right)}\right)$

$, for\ f \in [1,3]$

To calculate fishing mortality encountered by a population unit $F_{a,t,p}^{B}$ a combination of Eqn 26 and Eqn 16 has to be solved. This results in Eqn 27 where a solution is only valid if $F_{a,t,p}^{B} \geq 0$ and $F_{a,t,f}^{F} \geq 0$.

(Eqn A27)

$$\left(\sum_{f\in[1,3]} \left(\sum_{a=r}^{q} N_{a,t,p}^{B} A_{a,t,p,f} \frac{F_{a,t,f}^{F}}{F_{a,t,f}^{F} + M_{a,t,p}} \left(1 - e^{-F_{a,t,f}^{F} - M_{a,t,p}}\right) W_{a,t,f}^{F}\right) - \sum_{a=r}^{q} N_{a,t,p}^{B} \frac{F_{a,t,p}^{B}}{F_{a,t,p}^{B} + M_{a,t,p}} \left(1 - e^{-F_{a,t,p}^{B} - M_{a,t,p}}\right) \sum_{f\in[1,3]} (A_{a,t,p,f}\, W_{a,t,f}^{F})\right) = 0$$

$, for\ p \in [1,3]$

Symbols used in equations

	Parameter	**Definition**
Historic population dynamics	$N^{S}_{a,t,f}$	Numbers of fish, as obtained from a stock assessment, at age *a* at the start of year *t* in fishing area *f* (^{S} denotes stock)
	$N^{B}_{a,t,p}$	"Biological / true" numbers of fish at age *a* at the start of year *t* in population unit *p* (^{B} denotes biological)
	$A_{a,t,p,f}$	Proportional availability of numbers of fish at age *a* in year *t* in population unit *p* to fishery *f*
Population dynamics	$Z^{B}_{a,t,p}$	Total mortality of the "biological / true" population unit at age *a* in year *t* in population *p* (^{B} denotes biological)
	q	Age of the plus group; in this study, *q*= 8 years
Mortality rates	$F^{F}_{a,t,f}$	Fishing mortality at age *a* in year *t* as imposed by fishery *f* (^{F} denotes fishery)
	$Sel^{F}_{a,\bar{t},f}$	Mean selection pattern at age *a* in year *t* of fishery *f* (^{F} denotes fishery)
	$E_{\bar{t},f}$	Mean effort in year *t* of fishery *f*
	$Q_{\bar{t},f}$	Mean catchability in year *t* of fishery *f*
	$F^{B}_{a,t,p}$	Fishing mortality at age *a* in year *t* as encountered by population unit *p* (^{B} denotes biological)
	$M_{a,t,p}$	Natural mortality at age *a* in year *t* as encountered by population unit *p*
	$\left(\sigma^{Sel}_{a.f}\right)^2$	Variance of the selection pattern at age *a* in fishery *f*
Weights at age	$W^{F}_{a,t,f}$	Body mass of the average individual in the catch at age *a* in year *t* of fishery *f* (^{F} denotes fishery)
	$Winf^{F}_{f}$	Asymptotic weight of the average individual in the catch of fishery *f* (^{F} denotes fishery)
	K^{F}_{f}	Growth coefficient of the average individual in the catch of fishery *f* (^{F} denotes fishery)
	$t0^{F}_{f}$	Length at birth of the average individual in the catch of fishery *f* (^{F} denotes fishery)
	a, b	Length-weight conversion factors
	$\overline{W^{F}_{a,f}}$	Average body mass of the average individual in the catch at age *a* of fishery *f* (^{F} denotes fishery)
	$\left(\sigma^{WF}_{a,f}\right)^2$	Variance of the average body mass at age *a* in fishery *f* (^{F} denotes fishery, ^{W} denotes weight)

	$W^S_{a,t,f}$	Body mass of the average individual at age *a* in year *t* in stock *f* (^{S} denotes stock)
	$Winf^S_f$	Body mass of the average individual at age *a* in year *t* in stock *f* (^{S} denotes stock)
	K^S_f	Growth coefficient of the average individual in stock *f* (^{S} denotes stock)
	$t0^S_f$	Length at birth of the average individual in stock *f* (^{S} denotes stock)
	$\overline{W^S_{a,f}}$	Average body mass of the average individual at age *a* in stock *f* (^{S} denotes stock)
	$\left(\sigma^{WS}_{a,f}\right)^2$	Variance of the average body mass at age *a* in stock *f* (^{S} denotes stock, ^{W} denotes weight)
	$W^B_{a,t,p}$	Body mass of the average individual at age *a* in year *t* in population unit *p* (^{B} denotes biological)
	$Winf^B_p$	Body mass of the average individual at age *a* in year *t* in population unit *p* (^{B} denotes biological)
	K^B_p	Growth coefficient of the average individual in population unit *p* (^{B} denotes biological)
	$t0^B_p$	Length at birth of the average individual in population unit *p* (^{B} denotes biological)
	$\overline{W^B_{a,p}}$	Average body mass of the average individual at age *a* in the population unit *p* (^{B} denotes biological)
	$\left(\sigma^{WB}_{a,p}\right)^2$	Variance of the average body mass at age *a* in population unit *p* (^{B} denotes biological, ^{W} denotes weight)
Catch equations	$C^F_{a,t,f}$	Catches at age *a* in year *t* of fishery *f* (^{F} denotes fishery)
	$C^B_{a,t,p}$	Catches at age *a* in year *t* of population unit *p* (^{B} denotes biological)
Stock-recruit relationship	$\propto_p$ β_p	Constants of population unit *p*
	$SSB_{t,p}$	Spawning-stock biomass of population unit *p* in year *t*
	r	Age of recruitment, here r = 1
	$\sigma^{SRR}{}^{2}_{p}$	Variance of recruitment of population unit *p*
Spawning-stock biomass	$O^B_{a,t,p}$	Proportion mature at age *a* in year *t* in population unit *p* (^{B} denotes biological)
Survey indices	$I_{a,t,p}$	Survey index at age *a* in year *t* of population unit *p*
	$R_{a,p,g}$	Proportion of samples at age *a* identified as population unit *p* from population unit *g* (i.e. classification success)
	$P_{a,t,p}$	Number of samples at age *a* in year *t* that belong to survey index for population *p*

	Δ_j	Vector containing the values 0 and 1 identifying the samples that belong to population unit p
	$S_{j,t}$	Sample j of total sample distribution in year t
	$Sel^I_{a,t,f}$	Selection pattern of survey f at age a in year t (^{I} denotes indices)
	SI	Survey sample size
	IM	Identifier of population units being joined in the survey
	${\sigma^I}^2_{a,p}$	Variance of survey index at age a of population unit p (^{I} denotes indices)
TAC scenario	$T_{t,f}$	TAC in year t of fishery f
	$Ftarget_{t,f}$	Target fishing mortality in year t of fishery f
	$Sel^A_{a,t,f}$	"Assessed" selection pattern at age a in year t of fishery f (^{A} denotes assessed)