

SPATIALLY EXPLICIT POPULATION DYNAMICS MODELS FOR ANTARCTIC TOOTHFISH IN THE ROSS SEA REGION

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Abstract

Population modelling software was developed that captures the dynamics of spatial heterogeneity of the population along with age structure, movement and reproductive stage transition in a holistic framework. Using this software, three spatially explicit age-structured models were developed for the Antarctic toothfish (*Dissostichus mawsoni*) population in the Ross Sea region and used as operating models to evaluate the performance of single-area assessments. The models were generalised Bayesian population models and were optimised by fitting to fishery observations. Movement was parameterised using preference functions based on spatially discrete environmental layers. The shapes of the preference functions were established through iterative model testing whilst the parameters defining the preference functions were estimated within each model. The spatial structure of the models divided the Ross Sea region into 189 equal-area (24 000 km²) cells. The underlying spatial distribution of the population was either restricted to the 65 cells historically fished, to the 120 cells containing habitable depths, or to the entire Ross Sea region (all 189 cells). Estimates of movement rates were consistent with the results of tagging studies and fits to the other observations (age, reproductive development) were adequate. These operating models were then used to investigate potential biases of the current single-area stock assessment. Simulations based on the three spatial distribution scenarios suggested that the current single-area stock assessment is biased low by 19–43%.

Introduction

Most stock assessments used for management purposes around the world are single-area models. However, the spatial structure and movement of fish has shown the potential to have a strong influence on stock assessments (e.g. Quinn and Deriso, 1999; Welsford and Ziegler, 2013) and management outcomes, risking overexploitation of those stocks (e.g. Ying et al., 2011).

Spatially explicit stock assessments have been limited in applications (see Goethel et al., 2011, for a review). They have high computational and data

requirements, making them unsuitable for all but the most data-rich stocks. The modelling of movement of fish populations between areas has generally been either where migration between the areas is estimated as an area-specific process (e.g. Goethel et al., 2014) or where movement is modelled as an advection-diffusion or ‘gravity’ process (e.g. Sibert et al., 1999). To model movement across x areas, the first approach typically requires a set of parameters of order x^2-x and is generally only suitable for modelling a small number of discrete areas. The second approach requires fewer parameters (typically order x) but has less flexibility to model complex movement patterns. Implementations of

one or the other of these methods are available in various stock assessment modelling software packages including AD Model Builder using MAST (Fournier et al., 2012), CASAL (Bull et al., 2012) and SS3 (Methot and Wetzel, 2013). Spatial movement models of fish populations have been used in a wide variety of applications, including the assessment of stocks that inhabit, or move between, multiple areas (e.g. Punt and Walker, 1998; Goethel et al., 2014), development of bio-climate envelope models to consider population responses to climate change (e.g. Cheung et al., 2008) or spatially explicit predator–prey interactions.

In order to alleviate the issue of dramatically increasing numbers of estimable parameters with numbers of spatial areas, Bentley et al. (2004b) developed the concept of habitat preference curves, where the distribution and inferred movement of fish in different areas was related to preference functions for environmental variables. Such parameterisation allows the movement of fish between numerous areas with fewer parameters needed than if the movement between each of the areas was estimated. Dunn and Rasmussen (2008) devised software for spatially explicit population modelling (SPM) that allows for a wide range of spatial models to be implemented and evaluated. Movement functions available are migration between cells, diffusion and preference movement. The program structure, assumptions and technical details of SPM are described in the SPM user manual (Dunn et al., 2012a). In brief, SPM can be used to implement aggregate movement models that include a spatially explicit statistical catch-at-age population dynamics model. SPM incorporates a discrete time-step state-space model that represents a cohort-based population age structure in a spatially explicit manner. It can model both population processes (i.e. ageing, recruitment and mortality) and movement processes defined as the product of a set of preference functions that are based on known attributes of spatial location (e.g. depth). In addition, SPM can be used either as an estimation model or as an operating model for simulation of observations in, for example, management strategy evaluations (Butterworth, 2007; de Oliveira et al., 2008). SPM was used to develop spatial models of the Antarctic toothfish (*Dissostichus mawsoni*)

population in the Ross Sea region, and to infer potential bias of the current single-area stock assessment used for management purposes.

The Antarctic toothfish exploratory fishery in the Ross Sea region was initiated in 1997¹. The fishery has operated during the summer months, and annual catches have averaged about 2 700 tonnes since 2003. The catch limits for Antarctic toothfish in the Ross Sea region have been based on the yield estimates from a single-area Bayesian sex- and age-structured statistical catch-at-age assessment model using CASAL software (Bull et al., 2012). Stock assessments for the Ross Sea region have been carried out since 2007, and most recently in 2013 (Mormede et al., 2013a). The data within the assessment model include the total catch, catch-at-age frequencies and annual tag-release and recapture data from the fishery tagging program. Estimates of stock status were mostly informed by the tag-release and tag-recapture data.

An important assumption of the use of the tag-release and recapture data is that the probability of recapturing a tagged fish is the same as that of an untagged fish, irrespective of the location at which tagged fish were released or the subsequent spatial distribution of fishing effort from which fish were scanned to detect recaptures. Conceptually this requires either homogenous mixing of tagged and untagged fish in the population, or that fishing effort patterns have been distributed such that removals were proportional to the underlying abundance of fish in each location.

The area available for fishing in the Ross Sea region is constrained by areal closures (approximately 70% of the total region), local area catch-limits, by-catch move-on rules and highly variable access to open areas due to sea-ice extent. Hence, in some years the fishing effort can be either constrained in space or distributed into less frequented areas. This spatial heterogeneity, combined with the relatively short average annual distances moved by Antarctic toothfish (median of about 20 km after a year at liberty, see Parker et al., 2013), suggests that the assumption of complete mixing of tagged and untagged fish in the fished population is likely to be violated at least in the short term. Such violations

¹ Note that the CCAMLR management season is from 1 December to 30 November. In this report, the term ‘year’ refers to the period in which most of the season occurs, e.g. the period 1 December 1996 to 30 November 1997 is labelled the 1997 year.

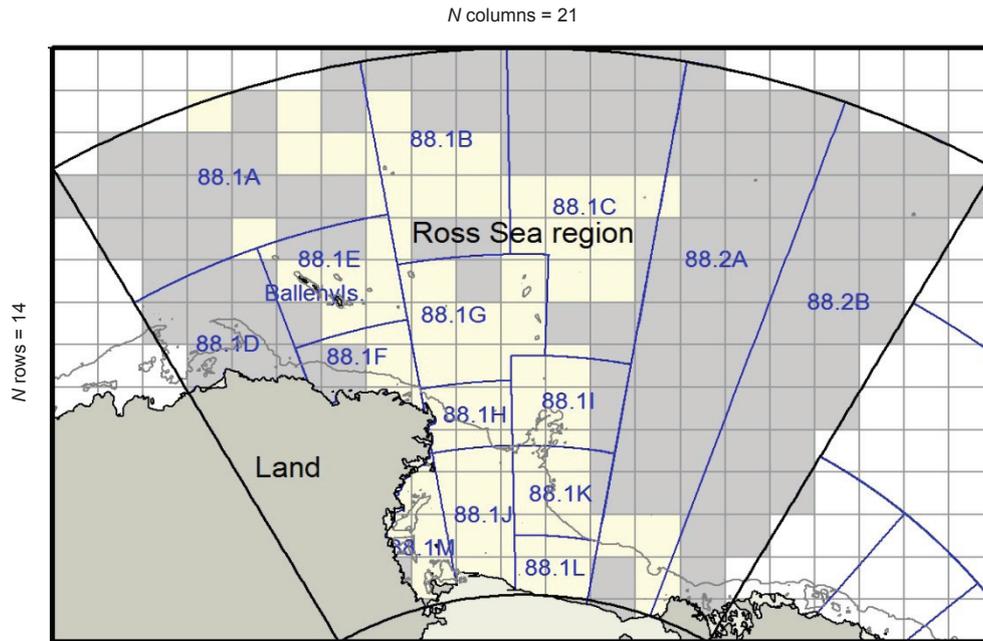


Figure 1: Spatial grid representation of the Ross Sea region used for the spatial models (bounded region). Cells where fishing has occurred are shown in yellow. The CCAMLR small-scale research units (SSRUs) used for management are shown in blue and the 800 m depth contour in grey, which represents the border between the continental shelf and slope areas.

may lead to bias in the stock assessment results (e.g. Hoenig et al., 1998; Pollock et al., 1991; Welsford and Ziegler, 2013).

The aims of this paper were two-fold. The first was to develop spatially explicit operating models for Antarctic toothfish in the Ross Sea region based on the spatially explicit observational data available. This was then used to test a number of movement hypotheses parameterised by alternative spatially explicit environmental variables, such as distance to the Antarctic Circumpolar Current (ACC). Tag-release and tag-recapture data and observation data, such as age composition and reproductive state, were used to estimate parameter values for movement functions for three operating models that describe plausible spatial population distributions of Antarctic toothfish.

Second, these models were used to evaluate potential bias in estimates of stock size from the current single-area Ross Sea assessment model (Mormede et al., 2014). Here, observations from the three spatial operating models were simulated and these data were then used as inputs into the single-area stock assessment model described by Mormede et al. (2014) to evaluate potential biases relative to the ‘known’ simulated population.

Methods

Three spatially explicit, age-based, single-sex operating models were developed using SPM. Although toothfish have slightly different biological characteristics by sex, these are expected to be small compared with the approximations in the estimation of spatial movement. Hence these models were single-sex in order to reduce complexity, parameterisation requirements and model run times. The overall structure of the models followed the life cycle of Antarctic toothfish initially described by Hanchet et al. (2008) and refined by Parker and Marriott (2012) and larval dispersion modelling (Dunn et al., 2012b). As explained below, the model captured the ontogenetic movement whereby small fish (age 2) recruit to the Ross Sea shelf (shallower than 800 m depth). As they age and grow, they move across the Ross Sea shelf and onto the continental slope (into water deeper than 800 m) before maturing and migrating to the northern areas (seamounts, banks and ridges) to spawn. This was represented within the model using five reproductive categories: immature, mature, pre-spawning, spawning and post-spawning.

Spatial structure

The spatial structure of the models was represented by dividing the Ross Sea region into a rectangular grid of 14 rows and 21 columns (Figure 1). Each cell was 24 336 km² (i.e. equal-area squares with side lengths of 156 km), resulting in 189 cells (over ocean) where the population could potentially be present, of which 65 have been fished on at least one occasion since the fishery began. Each cell represents the part of the overall population that occurs in that geographical area. The choice of scale was a trade-off between reproducing the required spatial complexity, the available data and the time the model took to run. For example, investigative models containing 60 cells were quick to run but could not capture the movement processes well, whilst models containing 1 650 cells captured the spatial heterogeneity better but were too slow (weeks to months) to be useful as a developmental tool.

Three models of the potential spatial distribution of the Ross Sea toothfish population were considered. The first model assumed it was restricted to those cells that have been fished and have recorded a catch of toothfish on at least one occasion historically (65 cells – restricted model). The second model assumed that the population was restricted to those cells which comprised suitable toothfish habitat (120 cells – semi-restricted model). Note that no observations of toothfish outside the area historically fished exist, therefore the semi-restricted model assumes toothfish may exist in locations of suitable habitat where no observations exist. The third model assumed that the population could extend across the entire marine area within the Ross Sea region regardless of suitable habitat (189 cells – unrestricted model). For the purposes of this scenario, suitable habitat was defined as cells where at least 5% of the bottom depth strata was between 450 and 2 820 m based on GEBCO depth (see also Figure 2c).

Population processes

Within each spatial cell, the number of toothfish in the population model aged 2 to 30 was recorded separately, with a plus group at age 30. Also recorded was the population at each reproductive category (immature, mature, pre-spawning, spawning and post-spawning) separately for untagged and tagged fish. Splitting the population

into reproductive categories was necessary in order to capture the differing movement behaviours of each category (Hanchet et al., 2008). The year was split into two half-year time steps, plus one instantaneous time step for aging and the movement of spawners back to the grounds occupied by mature fish (Table 1).

The population was initialised at an equilibrium state, by first applying recruitment, spawning, maturation, natural mortality and ageing processes for a 100 year period. In this phase, movement was not permitted. In the second initialisation phase, for a further 101 years, movement processes were added to the population processes. Splitting the initialisation process into two phases, with the first phase limited to population processes and the second phase introducing movement, improved minimisation time. Convergence to an equilibrium was tested with the test statistic Δ , defined as the sum of absolute differences as a proportion of total abundance between successive years, i.e.

$$\Delta = \frac{\sum_{ijkl} |a_{2,ijkl} - a_{3,ijkl}|}{\sum_{ijkl} a_{2,ijkl}},$$

where a_2 is the value of cell (i,j) for category k at age l at the end of the 100th year of the second initialisation phase, and a_3 the respective value at the end of the 101st year. (Note that perfect convergence would result in $\Delta = 0$.) Following initialisation, the spatial model was run for a period of 17 model years, from 1995 to 2011. Fishing mortality (from 1998) and tagging processes (from 2001) consistent with historically reported catches and tagging rates in the history of the Ross Sea fishery were applied in addition to the population and movement processes that were applied during the second initialisation phase.

The number of recruits in the first year was parameterised by R_0 . Fish recruited at age 2 to the immature category were assumed to be uniformly distributed in those cells with a depth of less than 800 m (throughout the Ross Sea shelf). For the purposes of these scenarios, the number of recruits in the initial year of the model was assumed fixed and set at the value estimated by the 2011 stock assessment of Antarctic toothfish, i.e. $R_0 = 1.02 \times 10^6$ (Mormede et al., 2014). The stock–recruit relationship was assumed to follow a Beverton-Holt

Table 1: Timing of the population processes and associated modelling parameters (processes in italics are transition processes, and parameters with * are estimated in the model). The number of parameters estimated includes the α parameter where applicable.

Time-step	Processes (in order of occurrence)	Details of modelling process	Number of parameters estimated
Summer	Recruitment	To age 2+	-
	<i>Immature</i> \rightarrow <i>mature</i>	Age-based logistic ogive*	2
	<i>Mature</i> \rightarrow <i>pre-spawning</i>	Constant rate*	1
	Natural mortality	Half applied in this time-step	-
	Fishing mortality	Catches, fishing selectivity* (logistic), catchability* (constant)	2 + 1
	<i>Un-tagged</i> \rightarrow <i>tagged</i>	Numbers, tagging selectivity* (double normal)	3
Winter	Natural mortality	Half applied in this time-step	-
	Movement of immature	Function of distance* (exponential), depth* (double-normal)	1 + 4
	Movement of mature	Function of distance* (exponential), depth* (double-normal), habitat* (linear), and hills* (categorical)	1 + 4 + 2 + 2
	Movement of pre-spawners	Function of distance* (double-normal), temperature* (double-normal), hills* (categorical)	4 + 4 + 2
	<i>Pre-spawning</i> \rightarrow <i>spawning</i>	Fixed rate of 1	-
	Spawning	-	-
Spring	<i>Spawning</i> \rightarrow <i>post-spawning</i>	Constant rate*	1
	Movement of post-spawners	Distance (pre-spawners function), depth and habitat (mature functions)	-
	<i>Post-spawning</i> \rightarrow <i>mature</i>	Fixed rate of 1	-
	Ageing of all categories	All age by one year (30+ remain 30+)	-
Total	16 processes		34

relationship with steepness $h = 0.75$, as was assumed in the stock assessment (Mormede et al., 2014), to allow comparisons among models.

Natural mortality (M) was applied as an instantaneous rate and was assumed to be 0.13 y^{-1} based on the analysis of fishery age-frequency data using several methods (Chapman and Robson, 1960; Hoenig, 1983; Punt et al., 2005), and adopted by CCAMLR for use in the stock assessment (WG-FSA-SAM, 2006). Natural mortality was applied as two mortality processes of 0.065 y^{-1} with fishing mortality applied in-between. Fishing mortality was assigned to each spatial cell in each year based on the number of toothfish reported in each year from fisheries data for the years 1998–2011. The maximum exploitation rate was assumed to be $U_{max} = 0.9$, so that spatial model estimates that resulted in cell abundance values that did not allow the known catch to be taken would not be permitted.

Category transitions that moved fish between immature, mature, pre-spawning, spawning and post-spawning categories were applied to allow the different movement behaviours of ontogenetic movements and of fish migrating to and from spawning areas. In this model, five category transitions were defined. These were:

Immature \rightarrow *mature*: transition rate of immature to mature fish, defined as an age-based logistic ogive, with parameters estimated by the model. The maturation ogive was parameterised by the parameters a_{50} and a_{1095} , and represented the proportion in each age class that mature at each age class.

Mature \rightarrow *pre-spawning*: transition rate of mature fish to pre-spawning fish. Defined as a constant rate p_{spawn} , estimated in the model (i.e. p_{spawn} of the fish categorised as mature become pre-spawners). This parameter allowed us to mimic the potential for skip-spawning of mature fish, by not forcing 100% of mature fish to spawn in each year (Parker and Grimes, 2010).

Pre-spawning → *spawning*: transition of all pre-spawning fish to spawning fish. Defined as a rate of 1 (fixed), so that all fish that are denoted as pre-spawning are assumed to spawn. This allows the model to distinguish between pre-spawning fish which can move and spawning fish which do not move.

Spawning → *post-spawning*: transition rate of spawning fish to post-spawning fish. Defined as a rate p_{mature} , estimated in the model (i.e. p_{mature} spawning fish were assumed to return to a post-spawning (non-spawning) state). This allows for the migration of spawners back to mature (feeding) areas, and allows the potential for fish to spawn more than one year in a row (i.e. those fish that do not undergo the transition in a particular year) when $p_{mature} < 1$.

Post-spawning → *mature*: transition of all post-spawning fish to mature fish. Defined as a rate of 1 (fixed), so that all fish that are denoted as post-spawning revert to mature fish which can then transition to pre-spawning again in a future time step.

Un-tagged → *tagged*: transition of a specified annual number of fish to a tagged state. Defined as a transition of an annually specified number of fish, and set equal to the number of fish tagged each year per individual cell based on tag-release data. Age and reproductive category structure was applied by assuming that fish tagged in each cell were distributed across ages and categories proportional to the number in each age and category of untagged fish in each cell, after applying double-normal fishery selectivity (estimated). According to CCAMLR rules, fish are tagged in proportion to the full size distribution of the catch. Note that initial tag mortality, annual tag-shedding and tag-related growth retardation assumed to occur in the full assessment models were ignored, although these could be included as required for specific simulation experiments.

The fishing selectivity was defined as an age-based logistic ogive for the entire fishery, with parameters estimated by the model. It was parameterised by the parameters a_{50} and a_{1095} , and represented the proportion in each age class that was available to the fishing gear in each year. This option was preferred to a double-normal curve where cryptic biomass is allowed, since it was assumed that the model captures the entire spatial

distribution of the stock and therefore cryptic biomass is explicitly taken into account spatially. No separation was made between autolines and Spanish-line systems, even though their selectivities are slightly different, in order to limit the numbers of parameters estimated and reduce data fragmentation.

The timing of the population processes and associated modelling parameters are given in Table 1.

Movement processes

The movement processes were assumed to occur simultaneously over all cells (synchronous updating) and were implemented as habitat-based preference functions. These were based on environmental attributes for each spatial cell. A number of potential environmental habitat layers were tested to check their suitability in explaining fish distribution, such as distance from the ACC or current flow (e.g. Mormede et al., 2012), but were later superseded with better-fitting environmental variables. The environmental habitat layers which resulted in the best-fitting models are shown in Figure 2. They were as follows:

- median depth, based on the median depth of each cell as calculated from GEBCO one minute grid (BODC, 2010) (shallow regions) and Smith and Sandwell (1997) (deeper regions) bathymetric data sets, while ignoring any areas above sea level
- temperature at 500 m depth from the World Ocean Atlas, 2009 (Locarnini et al., 2010)
- proportion of potential habitat in each cell defined as the proportion of cell area between 450 and 2 870 m based on GEBCO depth. The upper limit (2 870 m) was the 95th percentile of GEBCO depth in the locations where fishing has occurred
- a binary variable defining whether a cell included hills or not, derived from GEBCO depth. A cell was defined as having hill habitat if more than 75% of seabed area was deeper than 2 000 m and at least 5% of the area in the cell was shallower than 2 800 m

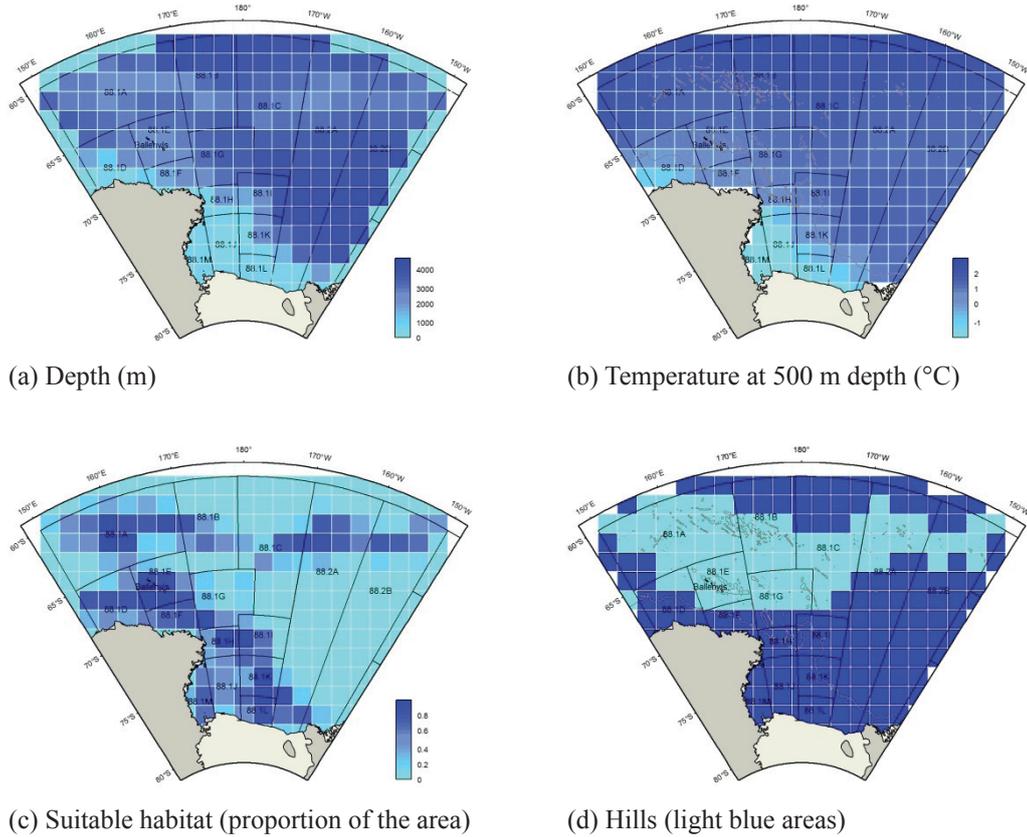


Figure 2: Environmental habitat layers used in the optimised spatial models.

- the distance between cells, calculated as the Euclidean distance (in kilometres) between the centres of each cell.

The amount of movement between any two cells was then assumed to be equal to the scaled weighted product of all preference functions, with weights α (essentially acting as a variable that allows modification of the relative importance of each individual preference function). Some values of α were fixed at 1 to avoid over-parameterisation of the model. The functions used in the final model are detailed in Table 1, along with the number of parameters estimated for each function and the order of the population processes. Further details on the preference movement process and equations used in SPM are given in Appendix 1. Other options for the habitat preference functions were investigated using different combinations of preference function shapes (e.g. double normal vs. exponential or logistic) and other environmental variables (e.g. distance from the Antarctic Circumpolar Current) in alternative models. The model structure presented here represented the model that

when fitted had the lowest objective function value, after taking into account the number of parameters in each model.

Observations

No research survey data on abundance are available for Antarctic toothfish in the Ross Sea region to inform spatial distribution or relative abundance. However, as a CCAMLR exploratory fishery, it has comprehensive data collection protocols and all vessels have scientific observer coverage by both the Flag State as well as an international CCAMLR observer (Conservation Measure 24-01, paragraph 3(c), see CCAMLR, 2013). These data were used to derive six sets of spatially explicit fisheries-based observations for each spatial cell where fishing occurred in each year. The number of measurements used for the spatial model are summarised in Table 2, and the observations detailed below.

- total catch of Antarctic toothfish (weight of fish per cell and year as for all other data)

Table 2: Total annual catch (tonnes), and the number of observations (raw, unscaled) of the catch-at-age proportions, proportions mature (or spawning), tag-release, and tag-recapture data, for the years 1998–2011.

Year	Catch (tonnes)	Number of observations used to derive input data			
		Catch-at-age	Proportions mature or spawning	Tag-release	Tag-recapture
1998	36	1 743	-	-	-
1999	296	6 939	-	-	-
2000	752	14 081	-	-	-
2001	592	14 087	-	259	-
2002	1 355	16 612	831	684	1
2003	1 769	26 482	6 796	570	6
2004	2 178	47 855	5 695	1 268	7
2005	3 210	56 523	12 728	2 321	24
2006	2 967	33 965	8 043	2 710	41
2007	3 079	40 295	16 773	2 028	87
2008	2 250	29 038	15 352	1 857	128
2009	2 450	25 725	9 202	1 990	49
2010	2 872	29 668	15 876	2 873	182
2011	2 931	*	*	*	*

* Age-based data for 2011 were not included in the model as ageing data was not available for the 2011 season when the data sets were constructed.

- catch per unit effort (CPUE), calculated as the unstandardised catch of Antarctic toothfish in kg per 1 000 hooks from autolines and Spanish longlines (but excluding trotlines that form a small proportion of total sets and have different CPUE characteristics from autolines or Spanish longlines)
- scaled proportions-at-age of the commercial catch, derived using the scaled length frequencies for the catch from each spatial cell, and multiplied by an annual (unsexed) age-length key from the aged otoliths collected by observers
- scaled proportions mature (defined as having a gonadosomatic index (GSI) greater than 1%) and scaled proportions spawning (defined as having a GSI greater than 2.5%), estimated from the scientific observer biological sampling and multiplied by the age-length key described above. The choice of 1% for mature and 2.5% for spawning was based on an analysis by Parker and Marriott (2012)
- proportions-at-age of tagged and released fish, estimated from the length frequency of the released tagged fish, multiplied by the age-length key described above
- proportions-at-age of fish recaptured with a tag, estimated from the length frequency of the tagged recaptured fish, multiplied by the age-length key described above, as used in the stock assessment (Mormede et al., 2014) and ignoring within-season recaptures.

Estimation of operating model parameters

Movement, selectivity and maturity parameters for the operating model were estimated by fitting to fishery observations.

Proportions-at-age data from the commercial catch, by spatial cell and year, were fitted to the modelled proportions-at-age composition using a multinomial likelihood (Bull et al., 2012). Effective sample sizes for the proportions-at-age data were estimated using the methods described by Francis

(2011a, 2011b). Proportions-by-category observations were used for the proportions mature and the proportions spawning observations. The likelihood for these observations was implemented as a binomial likelihood. The tagged proportions-at-age data were fitted with the tag-release selectivity (assumed constant over all cells and years) using a multinomial likelihood. Effective sample sizes for tag releases were assumed to be equal to the observed numbers of tagged fish released in each cell. The numbers of tagged fish recaptured at-age data were fitted using a binomial likelihood. Effective sample sizes for tag recaptures were assumed to be equal to the observed numbers of fish scanned at each age in each cell.

For all spatial models, process errors (uncertainty added to the observations prior to fitting them in the model) were assumed at an effective sample size of 30 for catch-at-age observations, maturity and spawning observations, and tag release and recapture observations; with a CV of 0.3 for CPUE observations. Due to the complexity of the model, the choice of these parameters was difficult and was based on other stock assessments. These errors were assumed when fitting to the spatial data.

Penalties imposed on the spatial models were (i) catch-constraint penalties, and (ii) tag-release event constraint penalties. Both of these were imposed to constrain the model from returning parameter estimates where the population biomass in any cell was such that the catch from any cell from an individual year would exceed the maximum exploitation rate (defined as $U_{\max} = 0.9$), or where there were insufficient fish in a cell to tag for the tag-release events.

Plausible model parameters were estimated using maximum posterior density (MPD) estimates with the finite numerical differences algorithm (see Dunn et al., 2012a, for details). The MPD estimates were evaluated by minimising the total objective function. The objective function was the sum of the negative log-likelihoods from the data, negative-log priors and penalties that constrain the parameterisations. This resulted in three plausible operating models (see ‘Spatial structure’) which could then be used to run simulations.

Simulations

The three operating models (with fixed parameters and movement assumptions) as fitted above were then used to generate simulated observations. These generated the observations that might have been gathered if the operating model were a true representation of the fish population and movement patterns. Annual catch-at-age, tag-release and tag-recapture observations were simulated from the locations where the historical fishery had fished in proportion to effort, and then these observations were aggregated over shelf, slope and north areas separately. In all cases, the biomass in the population was assumed known, defined by the number of initial recruits $R_0 = 1.02 \times 10^6$ individuals (as above).

Each observation was simulated assuming the error distribution used to fit the data, i.e. tag-recapture data were simulated using a binomial likelihood at age; catch-at-age data were simulated using a multinomial likelihood. However, the error values for each observation were assumed to be similar to that of the single-area stock assessment (see Mormede et al., 2014), with catch-at-age process error of 150 (effective sample size) and tag-recapture dispersion of 1.2. The values of the process error and tag dispersion had been estimated in the stock assessment model using the method of Francis (2011a, 2011b).

Evaluation of bias in the stock assessment model

Simulated observations from the spatial models (see above) were used in a single stock assessment model to investigate potential bias such as potential incomplete mixing, and its effect on stock status estimated by the single stock assessment model. The stock assessment model (hereafter referred to as assessment model to separate it from the operating model) was a modified version of that used for the assessment of toothfish in the Ross Sea region in 2011 (see Mormede et al., 2014) for full details of that model). The assessment model used the same population parameters as in the operating model. It was a single-sex, single-area, age-structured, three-fishery population model, with a known catch history, tag releases and observations of catch at age and tag recaptures. The parameters estimated by the assessment model were initial biomass and the fishing selectivities for the shelf, slope and north

Table 3: Relative abundance of toothfish by SSRU in 1995, in numbers and biomass, as a percentage of the entire population, for the three operating models. Also shown is the mean weight per individual fish by SSRU in kg. Note that SSRUs 882A and 882B are split at 67°S into north and south areas as habitats are different north and south of this latitude and comparable with the regional splits within the Ross Sea. ‘Other’ represents population in adjacent areas.

SSRU	Unrestricted model			Semi-restricted model			Restricted model		
	Numbers	Biomass	Mean weight	Numbers	Biomass	Mean weight	Numbers	Biomass	Mean weight
881A	4.7	9.6	27.0	3.4	8.8	34.6	1.4	3.4	32.7
881B	2.1	4.9	30.0	1.8	4.4	31.5	3.2	7.8	32.0
881C	4.0	9.5	31.3	3.5	7.9	29.5	5.4	12.5	30.8
881D	5.9	4.2	9.4	2.1	4.3	27.4	0.0	0.0	-
881E	4.2	6.5	20.3	3.6	7.0	25.4	3.8	7.1	25.1
881F	2.6	3.1	15.6	2.8	3.9	18.4	3.1	4.8	20.4
881G	5.6	9.1	21.4	6.4	9.8	20.2	8.4	13.8	21.8
881H	4.9	3.2	8.7	6.9	4.6	8.9	8.2	6.5	10.4
881I	5.9	7.3	16.5	5.5	6.0	14.4	7.0	8.3	15.6
881J	7.9	3.5	5.8	11.3	5.5	6.5	12.4	6.8	7.2
881K	10.3	7.5	9.5	13.5	9.6	9.4	15.6	11.6	9.8
881L	9.6	4.1	5.7	8.6	4.4	6.8	9.7	5.3	7.2
881M	8.7	3.7	5.7	11.6	5.3	6.1	12.4	6.3	6.8
882A North	0.9	2.5	38.5	0.8	2.0	35.0	0.0	0.0	-
882A South	14.5	13.7	12.6	11.0	9.7	11.6	7.1	5.0	9.2
882B North	0.4	1.2	40.1	0.4	1.2	38.2	0.0	0.0	-
882B South	5.8	5.9	13.6	4.8	3.5	9.8	2.2	0.8	5.0
Other	1.8	0.3	2.3	2.0	2.2	13.8	-	-	-
Total	100.0	100.0		100.0	100.0		100.0	100.0	

areas. Again, as in the spatial operating model, tag shedding, tag loss, tag growth loss and tag mortality were not considered.

For each of the three operating models, 100 sets of simulated observations, aggregated over the spatial domain, were randomly generated and passed as observations to the assessment model run in CASAL (Bull et al., 2012). Then, for each set, initial biomass and the selectivities were estimated in an MPD run. The values of the estimated initial biomass (parameterised as initial recruitment, R_0) from the MPD runs with the simulated observations were compared to that used in the operating model ($R_0 = 1.02 \times 10^6$). Two measures were used for this comparison, the percent bias (%bias) defined as

$$\%bias = (\hat{\theta} - \theta) \frac{100}{\theta}$$

and the relative root mean squared error (%RMSE) defined as

$$\%RMSE = \sqrt{\frac{\sum_i (\hat{\theta}_i - \theta)^2}{n} \frac{100}{\theta}}$$

Results and discussion

Development of operating models

All three models provided similar fish distributions across the area at the SSRU level (Table 3), although differences among models were present at the cell level (Figure 3). Very low densities of fish were predicted in areas not previously fished. The differences between the abundance and biomass figures show the progression of the smaller and more numerous fish on the shelf to larger fish and less numerous fish on the slope and even larger fish but less numerous fish in the north. Therefore, abundance showed a decreasing gradient from south to north whilst biomass showed the highest values on the slope. These biomass and abundance plots should be regarded as relative population distribution plots because in this model structure the initial recruitment R_0 is fixed at the value estimated by the single-area model, which is likely biased low (see below). This pattern is also reflected in the mean weight of fish per SSRU (Table 3), increasing from the shelf to the slope area and highest in the north (SSRUs 881A–C).

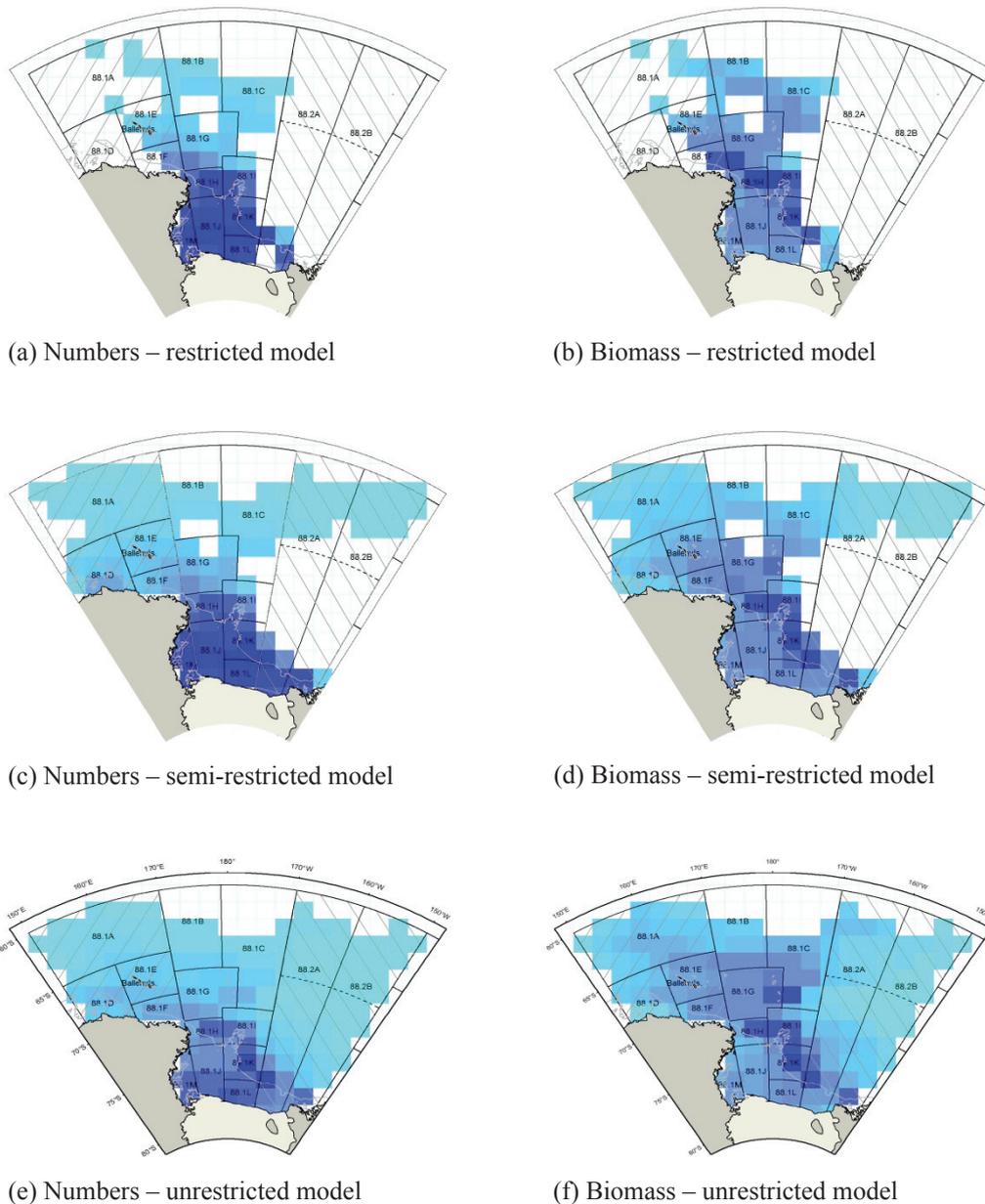


Figure 3: Distribution of the toothfish population as estimated by the restricted, semi-restricted and unrestricted spatial models, in numbers (left) or biomass (right). Scale is not shown as relative to total population, it is linear but different for each panel, light blue being zero and dark blue the highest value in the model. Dotted line shows the arbitrary split between the north and south areas of SSRUs 88.2A–B. The 800 m depth contour is shown in grey; it represents the limit between continental shelf and slope areas. Hatched SSRUs are currently closed to Olympic fishing.

The relative distribution of the population by SSRU is summarised in Table 3. The models broadly distributed relative biomasses and abundances in a similar fashion in areas open to fishing, with the spreading of fish to additional areas in the unrestricted model. The unrestricted and semi-restricted spatial models predict that 48–51% of the population by biomass is outside the SSRUs that are currently open, whereas the restricted model

predicts only 30% of the population outside the SSRUs that are currently open. SSRUs currently open are SSRUs 88.1 B, C, G, H, I, J, K, L.

In these models, immature, mature and pre-spawning fish have individual preference functions for specific environmental habitat layers, although not all are a function of the same layers (see Table 1). The functional forms of these preference

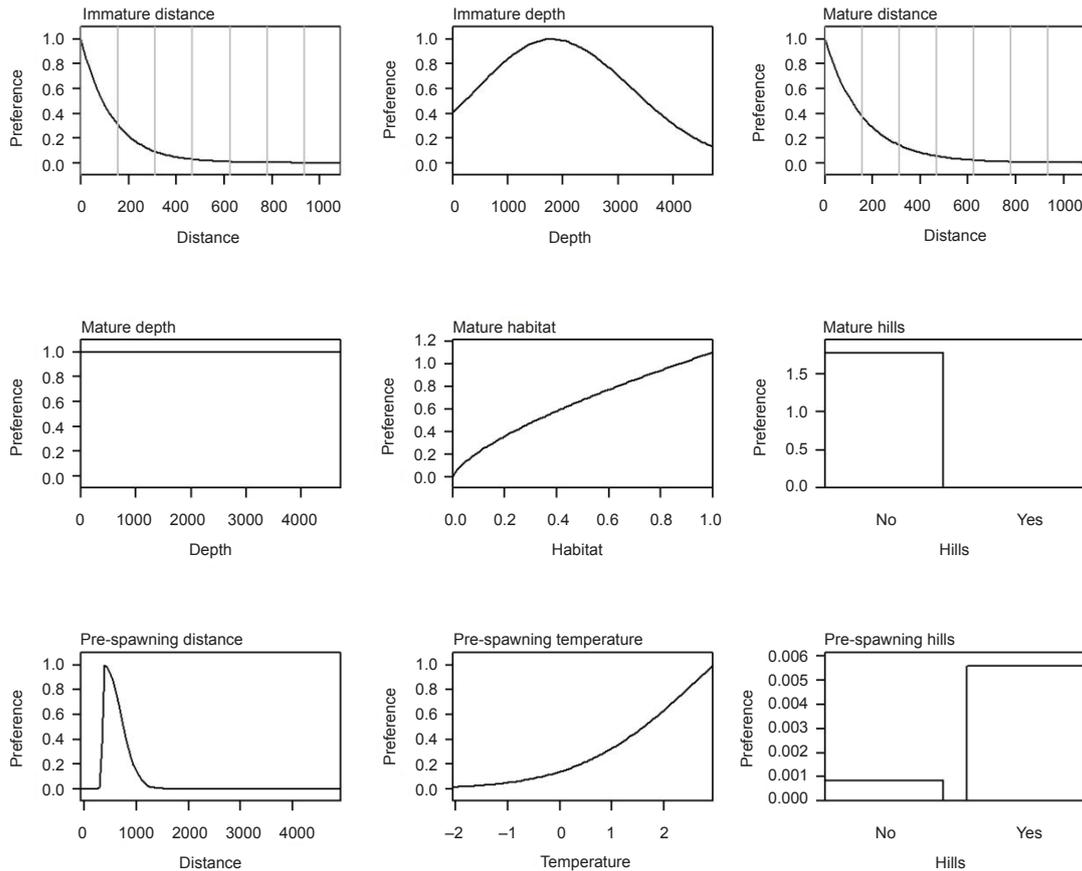


Figure 4: Estimated preference functions driving fish movements in the semi-restricted spatial model. Vertical lines in the distance preference functions indicate the width of individual model cells (156 km). Distance is expressed in km, depth in m, habitat in proportion suitable habitat and temperature in degrees centigrade.

functions were similar between the three spatial models, and all preference functions in the semi-restricted model are shown (Figure 4).

The spatial models show plausible toothfish population distribution and movements throughout the Ross Sea region: the spatial distributions of the immature, mature and spawning fish resulting from the spatial models broadly reflect the observed distribution patterns of these categories, with immature fish on the shelf, some mature fish on parts of the slope and some spawning fish in parts of the north. Individual movement preference functions are more difficult to interpret, as the actual movement will be a combination of multiple preference functions as well as dependent on the size of the cells at which the model is run. For example, movement functions show that 50% of immature fish might move over 100 km in a single year when the median movement of tagged and recaptured fish is about 30 km in a year (Parker et al., 2013). The discrepancy arises because fish in this model can

only move in increments of 156 km (the size of each cell) and that the actual movement of fish in each cell will be the combination of all preference functions.

The maturity and fishing selectivity ogives were similar for all three spatial models (Figure 5). The maturity ogive presents a similar 50th percentile maturity as female toothfish, but a much flatter curve than expected (95th percentile over 30 instead of 24 years). However, fixing the maturity ogive at the values used in the 2011 stock assessment (13 and 19.4 for 50th and 95th percentiles for males and females combined, see Parker and Marriott, 2012) resulted in a much worse fit of the spatial model to the maturity-at-age observations. Moreover, the maturity ogive of the spatial model represents the maturity of the entire population, including those in the north, when the maturity ogive used in the stock assessment was derived from fish on the slope only.

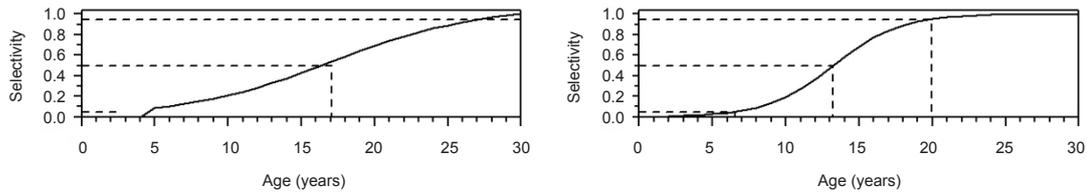


Figure 5: Maturity ogive (left) and fishing selectivity (right) estimated by the semi-restricted spatial model. Dashed lines indicate the 50th and 95th percentiles.

The optimised movement functions suggested that for all three spatial models about 50–53% of mature fish on the slope migrate to the north to spawn in any one year, and about 16–18% of the spawning fish in the north return to the slope in any one year. This could suggest that fish might skip spawning once every five years on average. A sensitivity analysis was carried out on the proportion of fish going to spawn, by fixing that parameter at a range of values and re-optimising the spatial model. Results showed that this parameter is poorly estimated, with the extreme of all fish migrating to spawn each year only providing a slightly poorer fit (about 200 points in the objective function) and values between 30% and 60% being almost equally probable (details available in Mormede et al., 2013b).

Model fits were similar for all three models. Fits to the data were adequate, although there was some indications of poor fit to the plus group of the proportions-at-age in the catch data, with the spatial models predicting more fish in the plus group than was observed. This may be a consequence of an underestimate of natural mortality (i.e. if the assumed value for M was lower than the true value), a declining right-hand limb selectivity in the fishery (the selectivity was assumed to be flat-topped in these spatial models), the need for further age classes (e.g. to age 50), or a spatial process whereby older fish are spatially distributed based on an environmental preference that was not modelled in the spatial models.

The proportion-mature-at-age fits also showed some structure in the residual patterns, with the spatial model predicting less fish mature for both young and old fish. This might suggest that the choice of a logistic maturity curve may be inadequate (and hence an asymmetric domed ogive may offer some improvements), or that a GSI threshold

based on fish sampled in summer, and uniformly in all locations, is not an appropriate index of maturity at the level of the Ross Sea region.

The most likely spatial model is the one that restricts toothfish distribution to depths which are known to provide suitable toothfish habitat, based on both the total objective function of each model, and the predicted location of toothfish biomass. The total objective function of the semi-restricted model was about 17 800 points, compared with about 24 800 points for both the restricted and unrestricted models. Moreover, as the models utilise fishery-dependent data only and have no information about the distribution of toothfish in areas where no fishing has occurred, the unrestricted spatial model could estimate fish movements into cells outside of the fished area, including those with implausible depths for toothfish. Despite this limitation, the semi-restricted and the unrestricted spatial models still showed similar patterns of toothfish distribution. This is in large part because the unrestricted spatial model estimated only low densities of fish occurring at depths beyond those known to provide suitable toothfish habitat. Therefore, even the unrestricted spatial model presents a plausible extreme distribution of toothfish in the Ross Sea region, with movement preference functions restricting fish to areas of plausible habitat.

Evaluation of bias in the assessment model

The unrestricted operating model estimated values of initial recruitment (and hence biomass) that were biased low by 43%; the restricted operating model estimated values of initial recruitment that were biased low by 17%; and the semi-restricted operating model estimated values of initial recruitment that were biased low by 32% (Table 4). This suggests that if the underlying spatial distribution of the population and movement functions for toothfish were as described by the operating models, then the assessment model was a

Table 4: Estimated R_0 , %bias and %RMSE for the three operating models.

Operating model	'True' R_0	Mean R_0 (90% credible intervals)		Estimated values	
				bias%	RMSE%
Unrestricted model	1.02×10^6	587 100	(488 300–738 900)	–43%	43%
Semi-restricted model	1.02×10^6	696 300	(563 600–890 000)	–32%	33%
Restricted model	1.02×10^6	843 500	(672 100–1 105 200)	–17%	22%

conservative estimator of the true state, especially when estimating biomass over the entire Ross Sea region. The RMSE values were generally similar to the bias values, showing little change in dispersion between operating and assessment models, with a slight increase in dispersion in the restricted operating model. However, only 100 simulations were used (due to the complexity and time required) and estimates of intervals may be uncertain.

Bias in the operating models is likely to reflect the mismatch in underlying distributions of tag releases and subsequent fishing effort, along with limited toothfish mixing between areas. The extent of the negative bias will depend on the proportion of fish in the unfished area and movement rates between fished and unfished areas. Current spatial operating models suggest that there is likely to be a substantial toothfish biomass in the Ross Sea region outside the current fishing footprint. Therefore, the single-area stock assessment model currently used for setting catch limits in the region is likely to be biased low, adding a conservative buffer to the management process in place.

Conclusions

In this paper, estimated movement preference functions were applied to three spatial population models of toothfish in the Ross Sea region. These models were then used to evaluate potential assessment biases arising from fish movements or from spatially heterogeneous patterns of fishing effort and/or tag releases. Underlying assumptions regarding fish movement and mixing of tags are an important drivers of the current single-area assessment of Antarctic toothfish in the Ross Sea.

Results show an ontogenetic movement of fish from the slope to the north, with smaller fish distributed on the shelf, larger fish on the slope and spawning fish on the northern hills. The preference functions suggest relative short distances moved

by immature and mature fish, whilst spawning fish moved larger distances. We applied simulated data from the spatial models to a single stock assessment model. The spatial operating models presented suggest that the single-area stock assessment of Antarctic toothfish in the Ross Sea is likely to be biased low by up to 43%. This shows that the spatial dynamics can be important for understanding bias in the assessment of stocks.

The spatial operating models presented here only include one set of plausible models for toothfish in the Ross Sea region. Further investigations in model structure could include alternative fishing ogives and mortality rates, defining an alternative index of maturity, use of a two-sex model and testing different movement scenarios. Further data collection would be useful to inform the parameterisation of future models, such as spatially representative gonad weight measurements, surveying likely spawning grounds during winter and obtaining fishery or survey data from areas not fished, or only lightly fished, to date.

While further analyses should be carried out and alternative movement hypotheses should be tested, simulation experiments using spatially explicit models can provide a useful tool to evaluate the direction and likely magnitude of potential bias and uncertainty in the understanding of area-aggregated stock assessments in general. If shown to be good representations of key population dynamics, they can also be useful to investigate the likely consequences for stock assessments of alternate management strategies, including changes in fishing effort distribution or tagging schemes. Such models can also be used to investigate the potential effects of alternative hypotheses of life history, for example maturity, on the resulting distribution of the stock.

The modelling framework applied, with the use of preference functions to parameterise fish movements between large numbers of areas, has allowed

the development of relatively complex spatial fish population models while avoiding the estimation of large numbers of parameters. In this instance, up to 189 areas were modelled using 24 movement parameters, but the model could be expanded to a larger number of cells using the same number of movement parameters if required to better capture any heterogeneity of the fishery. As a comparison, Taylor et al. (2011) modelled Atlantic bluefin tuna using up to 66 individual areas, and required either 66 movement parameters when modelled using an advection-diffusion process or 132 parameters when they estimated movement between all areas individually.

While the development and parameterisation of spatial models can be difficult, they do provide a method for developing operating models for evaluating assessment bias from spatial assumptions and their subsequent impact on management advice (Cope and Punt, 2011). Further, such approaches may also be useful for evaluating the impact of spatial management plans on fisheries or assessments. The further development of spatially explicit fisheries models will enable better management advice for stock assessment either directly or through their use as operating models in management strategy evaluation (MSE) (e.g. Butterworth, 2007; Constable et al., 2000; de Oliveira et al., 2008).

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**DESCRIPTION OF THE PREFERENCE MOVEMENT PROCESS
(EXCERPTS FROM THE SPM MANUAL, DUNN ET AL., 2012A)**

SPM implements three types of movement:

1. A migration movement rate of cohorts between any two locations, and is roughly analogous to movements between areas as implemented in other population models, such as CASAL (Bull et al., 2012).
2. Adjacent cell movement, parameterised by some function of an underlying layer – equivalent to, for example, movement processes implemented in Fish Heaven (Ball and Williamson, 2003).
3. Movement parameterised as a probability density function. Here, the key underlying idea is that the spatial distribution of cohorts at any point in time and at any location can be represented as a density function based on attributes of that location, local abundance, and/or distance from their previous location (Bentley et al., 2004a, 2004b).

Preference movements allows movement from any cell a to cell b and is implemented as a function of the product of up to n independent preference functions. We define the probability of moving from any cell a to any cell b as a function of the relative preference for that cell. Here, we use the term preference function (Bentley et al., 2004a 2004b) to describe the movement probability distributions.

We assume that the population and spatial extent are defined, and that there is a preference function that is a function of some (typically estimable) parameters and a spatially explicit set of known attributes. The preference function movement process allows the number of parameters describing movement to be reduced, and results in a movement process that is some function of some underlying property of each location for a given category of fish. For example, if we assume that movement between areas was a function of the Euclidean distance between areas, we could model movement between any two areas as a linear decay or exponential decay function. Alternately, if distribution and density were correlated with bathymetric depth for a marine organism, we might model the movement and distribution as a function of depth.

Movement in SPM can be defined as a probability distribution based on an underlying preference function. Here, we define the preference for a cell x as the preference function $f_x(\theta_x, P(x))$, where $\theta(x)$ are the parameters for f_x . So, given a set of n attributes for cell x , we can define a preference function for each, and hence we define the aggregated or total preference function for any cell x as the weighted product of individual preference functions,

$$P_x = f_1(\theta_1, P_1(x))^{\alpha_1} \times f_2(\theta_2, P_2(x))^{\alpha_2} \times \dots \times f_n(\theta_n, P_n(x))^{\alpha_n}$$

where α_i is an arbitrary weighting factor for attribute i . In order to avoid over-parameterisation, it is recommended that at least one α_i be fixed to the value of one.

Then we define the probability of moving from cell a to any cell b (where b is defined as the set of all possible cells, including a),

$$p(a \rightarrow b) = \frac{P_a}{\sum_{i \in \forall b} P_i}$$

Note that there are three forms of preference function:

1. Those that are a function of some underlying attribute of a cell, as defined by some spatially explicit layer L .

2. Those that are a function of the abundance (perhaps with a selectivity and for a subset of all categories) of each cell.
3. Those that are a function of the distance between the sink and the source cells.

Preference functions of the first type are determined only by the parameters of the preference function and some underlying, fixed, attribute. Preference functions of the others are dynamic, i.e. they depend on the relative locations of the cells or on the density of a cell at a particular point in time.

