



# Comparing spatial distribution modelling of fisheries data with single-area or spatially-explicit integrated population models, a case study of toothfish in the Ross Sea region

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## ABSTRACT

Most models used for assessing the status of fish stocks and providing quantitative advice for fisheries management are not spatially explicit despite the well-known spatial heterogeneity of fish populations. Statistical spatial distribution modelling, which can derive spatially-resolved biomass from catch rates, is a method increasingly used to infer trends in population biomass, particularly where integrated population models are not available. Although the spatial distribution modelling tool VAST was developed to analyze survey data, such methods have also been used with fisheries-dependent catch and effort data, particularly when survey data are not available. We developed a statistical spatial distribution model for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region of the Southern Ocean using the VAST (Vector Autoregressive Spatio-Temporal model) approach. We based the VAST model on catch-rate (catch per unit effort) data from the long-line fishery and compared the biomass time series obtained to that of existing single-area and spatially-explicit integrated population models which have also been developed for this population. The time series obtained from the statistical spatial distribution modelling approach was highly variable between years, inconsistent with constraints imposed on population dynamics by biological parameters, and substantially different from biomass trends obtained from the integrated models. Although it has been used successfully in other analyses, in this instance, the spatial distribution modelling could not overcome fine-scale spatial and vessel-based variability in fishery catch rates to estimate the underlying abundance of toothfish at the scale of the Ross Sea region measurable with the more-informed integrated models.

## 1. Introduction

Although it has long been recognized that many fish populations are spatially heterogeneous, there has been a recent surge in research develop methods to account for the spatial dimension of populations in fisheries assessments (e.g. Thorson et al., 2015a; Lauretta and Goethel, 2017; Berger et al., 2017; Punt, 2019). There are many reasons for explicitly modelling spatial structure (Kerr et al., 2017; Punt, 2019) including to account for spatial variation in biological and ecological parameters, to provide spatially-resolved management advice (e.g. for Marine Protected Area assessment), to allow for seasonal migrations between areas, and to appropriately account for spatially-separate population components or sub-stocks.

The assessment of the size of a fish stock and its productivity requires many different types of data to be combined, including fisheries

data (e.g., catch, effort, catch-at-age, mark-recapture data), biological (e.g., growth, maturation), and ecological (e.g., natural mortality, stock recruitment relationship) information. It is now accepted that integrated analysis (Fournier and Archibald, 1982), where several types of data are used in a single analysis via joint likelihood functions is more powerful than the traditional approach of combining the results of separate analyses (Maunder and Punt, 2013). Integrated population models include biological processes but rarely include a spatial component, due to a combination of the paucity of spatially explicit data available, complexity of the analyses required, and the limited consensus on “best practice” approaches for spatially explicit modelling currently available (see reviews of Goethel et al., 2011; Punt, 2017, 2019). When space is included in integrated population models, it is often through fleets as surrogates for area, or a few areas with explicit movement estimated empirically between the areas or estimated using

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diffusion-type processes. Notable exceptions include the packages Seapodym (Lehodey and Senina, 2009) and SPM (Dunn et al., 2012; Mormede et al., 2014b) which can accommodate large numbers of cells and use preference functions to parameterize movement.

Alternative approaches to including spatial effects in assessing the sizes of fish stocks using integrated assessment models have been based on spatial analysis methods. For example, a suite of statistical tools for spatial distribution modelling (e.g. Elith and Leathwick, 2011; Yates et al., 2018) can be applied in fisheries management to estimate relative stock sizes. The statistical package VAST (Thorson, 2019) was initially developed to analyze spatial catch and effort from fisheries-independent stratified surveys (Thorson, 2014), and has more recently been applied to other data such as length frequency data (Thorson and Haltuch, 2018), fisheries-dependent data (Thorson et al., 2016) and community composition data (Thorson et al., 2017). Such spatial modelling methods are “statistical” rather than “ecological” in that they generally ignore constraints from biological parameters and rely instead on the information contained within the data to inform population dynamics.

In this paper we investigate how a spatial distribution modelling method compares with integrated population models in a real-world fisheries example. We carry out spatial distribution modelling of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region of the Southern Ocean using available fisheries-dependent catch and effort data with the statistical package VAST. We compare the population biomass trajectory obtained with that of a non-spatial CPUE standardization, an existing single-area integrated stock assessment model with areas-as-fleets currently used for the management of the stock (Mormede et al., 2014a), and a spatially-explicit integrated population model using the package SPM (Spatial Population Model, Dunn et al., 2012) developed to investigate the potential bias of the single-area integrated stock assessment model (Mormede et al., 2014b). This is a challenging test case because the analysis covers the initial development phase of the fishery when the spatial footprint as the fishery expanded, and because changes in sea-ice lead to substantial variability in the spatial patterns of fishing effort from year to year.

## 2. Methods

### 2.1. Study system

The stock used for comparison is the Antarctic toothfish (*Dissostichus mawsoni*, here referred to as toothfish) in the Ross Sea region of the Southern Ocean (Fig. 1). Toothfish have a circumpolar distribution south of the Antarctic convergence (60°S) and the number of reproductively-distinct populations of toothfish in the Southern Oceans is currently uncertain. However, several studies in the Ross Sea region using genetics, parasites, otolith microchemistry, stable isotopes, and movements of fish from tag-recapture data have concluded that toothfish in the Ross Sea region are likely to comprise a single stock (Hanchet et al., 2008, 2015).

Although it is primarily a demersal species, adult toothfish can be neutrally buoyant and may inhabit the pelagic zone at times during their life cycle (Near et al., 2003). Growth has been well documented (Horn, 2002; Horn et al., 2003) with fish reaching about 60 cm total length after five years and about 100 cm total length after ten years. Ages have been validated experimentally, and there is a significant difference in growth parameters between sexes (Horn, 2002; Horn et al., 2003; Brooks et al., 2011).

Hanchet et al. (2008) described the life history and stock structure of toothfish in the Ross Sea which includes ontogenetic movement (e.g., see Ashford et al., 2012; Hanchet et al., 2015). Adult fish are found mainly on the ridges and banks of the Pacific-Antarctic Ridge in the northern Ross Sea region. Eggs and larvae become entrained by the Ross Sea gyre and move either westwards, settling around the Balleny Islands and adjacent Antarctic continental shelf, or eastwards with the

Ross Sea gyre settling along the continental slope and shelf to the east of the Ross Sea. As the juveniles grow, they move west with the Antarctic coastal current, back towards the Ross Sea shelf. The fish move northwards as they mature, feeding in the slope region at depths of 1000–1500 m, where they gain condition before moving north onto the Pacific-Antarctic ridge to spawn. It is not known how long spawning fish remain in the northern area. It is currently thought that toothfish remain in the Pacific-Antarctic ridge region for up to 2–3 years (although this pattern may be different for males versus females) and then they move southwards back onto the shelf and slope where productivity is higher, and food is more plentiful.

The length and age at recruitment to the Ross Sea fishery is approximately 80 cm and age 5–7. Estimates of maturity were based on histological examination (Parker and Grimes, 2010). The natural mortality rate  $M$  was estimated by Dunn et al. (2006) using the methods of Punt et al. (2005).

A longline fishery for toothfish has been operating since 1997 in the Ross Sea region under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources, later referred as CCAMLR (Hanchet et al., 2014). The fishery is a high-seas, multi-national, single-target bottom longline fishery, with regional catch limits and bycatch move-on rules (Hanchet et al., 2014, 2015). Due to the remote nature of the fishery, almost all analyses rely on fisheries-dependent data. All vessels carry two observers onboard and follow stringent data collection requirements ([www.ccamlr.org](http://www.ccamlr.org)) to sample biological characteristics of the catch. Catch and effort data are reported for every set (fishing event). A fisheries-based mark-recapture program has been ongoing since 2004 and provides a primary (and CPUE independent) index of abundance used by the integrated models (Parker and Fenaughty, 2013).

### 2.2. Stock and spatial modelling

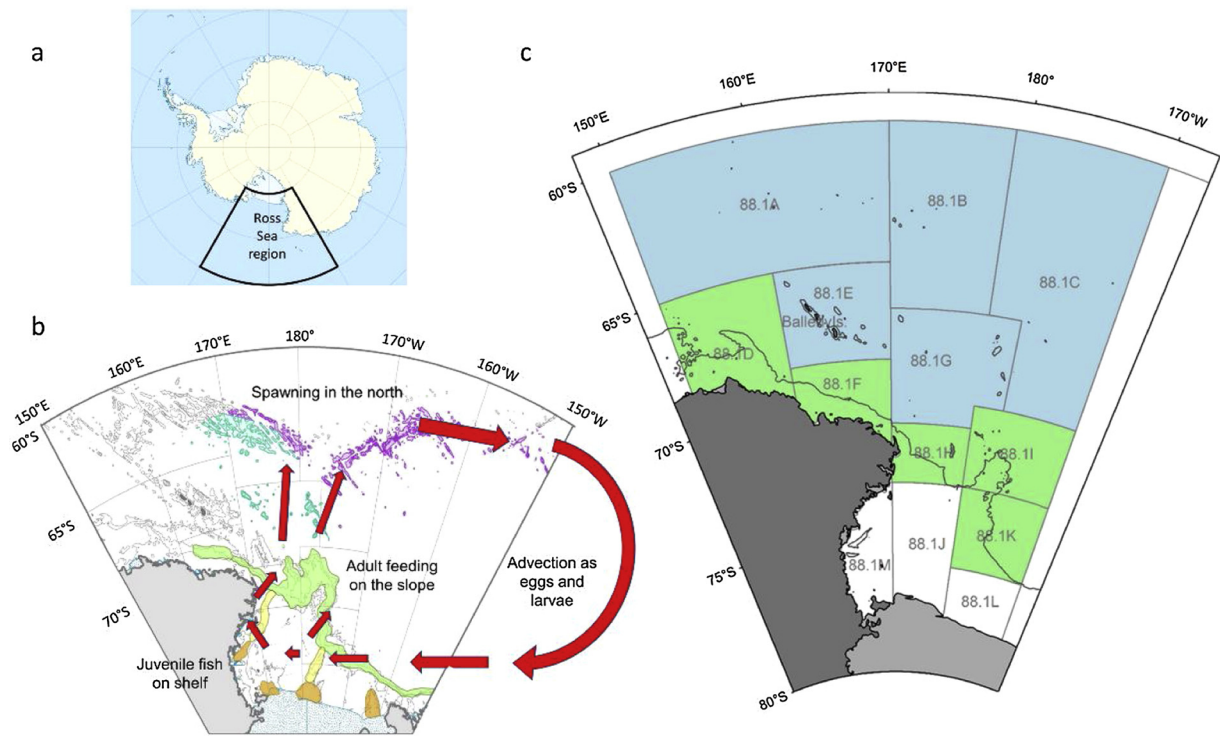
Three kinds of modelling approaches are compared in this study as described below and in Table 1. We summarize the data used in the various model types, the standardizations carried out if any, and the assumptions of the model, as well as the spatial component of each model. Only the results of fitting the VAST model are shown as fitting of the integrated model and SPM are available in other papers (respectively, Mormede et al., 2014a, b).

#### 2.2.1. CPUE analysis

Catch per unit effort (CPUE) was used in some of the modelling. Raw, or unstandardized, CPUE for the entire Ross Sea region is reported as an annual mean catch in kilograms per set, to allow for a non-linear relationship between the catch per line length or per hook if saturation occurs for example. CPUE was standardized through a generalized additive model (GAM) using the R package mgcv (Wood, 2017). Parameters evaluated in the regression were fishing depth (interquartile range or IQ 890–1350 m), soak time (IQ 14–30 h), line length (IQ 6–12 km), longline gear type (autoline, Spanish line, or trotline), fishing year, and statistical area (small scale research unit or SSRU, shown in Fig. 1c). Line length was used rather than number of hooks as a potential covariate as the configuration of the different types of longlines does not allow for a direct comparison using the number of hooks. Only significant parameters were kept in the final standardization ( $p \leq 0.01$  and  $r^2 > 0.05$ ).

#### 2.2.2. VAST spatial distribution modelling

Spatial distribution modelling was carried out using the R package VAST (Thorson and Barnett, 2017; Thorson, 2019) and applied to the raw catch and effort data. VAST (Vector Autoregressive Spatio-Temporal model) is a multivariate, mixed-effects model which can estimate values such as population density and its change through time for multiple locations, times, and species (e.g., Cressie and Wikle, 2011; Thorson, 2019). VAST is a multivariate development of the R package



**Fig. 1.** Study region. a: Ross Sea region; b: Schematic life-cycle of Antarctic toothfish in the Ross Sea region (Hanchet et al., 2008) showing juvenile fish on shelf (orange), juvenile shelf corridors (yellow), adult feeding areas on continental slope (green), spawning areas in the north (blue, purple), and key movement vectors (red arrows). c: Area of the single area integrated stock assessment model, where colors represent the three areas described as different fleets: shelf (white), slope (green), north (blue).

*SpatialDeltaGLMM*. This earlier package could fit single-species index standardization models which included both spatial variation that is constant among years (spatial effects) and spatial variation that varied among years (spatio-temporal effects) (Thorson et al., 2015b). Essentially, the model accounts for spatial correlation which has been shown to improve the index standardization of the stock (in this case toothfish in the Ross Sea region). Unlike integrated population models, spatial distribution models such as VAST have no knowledge of removals or

rates of growth of the population, but infer relative biomasses from catch rates, usually from fisheries surveys (Thorson, 2019).

In the present study, a VAST model was developed based on the raw catch rates (CPUE) of toothfish across the Ross Sea region. Thorson et al. (2018) recommends correcting for fisher targeting in the case of multispecies fisheries, but this is not applicable here as there is only one target species. Optimization of the model followed the recommendations of Thorson (2019) and was based on model performance tested

**Table 1**  
Structure and assumptions of the CPUE standardization (GAM) the spatial distribution model (VAST) the single stock population model (CASAL) and the spatial population model (SPM).

Model	GAM	VAST	CASAL	SPM
Number of cells	1	100-500	1	189
Movement	None	Spatial and temporal correlations	Three fisheries as areas	Immature, mature and spawning separately Preference functions by age of distance, depth, habitat, hills
Life history assumptions:		None		
Von Bertalanffy	None			
$t_0$			-0.256 (M); 0.021 (F)	-0.117
$k$			0.093 (M); 0.090 (F)	0.091
$L_{inf}$			169.07 (M); 180.20 (F)	174.545
CV			0.102	0.1
Growth				
$a$			1.38e-8 (M); 7.153e-9 (F)	1.05e-8
$b$			2.965 (M); 3.108 (F)	3.036
CV			0.1	0.1
Mortality ( $M$ )			0.13	0.13
Steepness ( $h$ )			0.75	0.75
Catches (removals)				Annual by cell
Data fitted to	CPUE	CPUE	Annual by area Mark-recapture Age frequency Juvenile survey data	CPUE Mark-recapture Age frequency
Standardization	Depth Line length Soak time Year	None significant	None	None

through the Akaike Information Criteria (AIC, Akaike, 1974) performance. The link function and probability distribution function were tested and those resulting in a parsimonious fit to the data chosen. The data contained complete records collected by observers and therefore represent the entire fishery. Sample sizes were constant between models. Bycatch data were used in the VAST model as a covariate to aid with standardizing the catch and effort data. In those models, each bycatch species (in numbers caught per set) was modelled as an additional species. Models were run adding a number of bycatch species or groups in decreasing order of numbers caught: (1) the top three species (toothfish, macrourid and icefish), (2) the top five species / species groups (i.e., adding *Antimora* sp. and skates), and (3) top ten species / species groups. The effect of the temporal correlations on the outcome was also tested by running various models with or without those correlations and comparing the AIC values of the models and the biomass trajectories.

### 2.2.3. Single-area integrated population modelling

A single-area integrated stock assessment was developed in 2005 using CASAL (Bull et al., 2012) and has been used by CCAMLR for management advice since 2006 (CCAMLR, 2017). The model fits annual age frequencies of commercial catch, juvenile age frequencies and biomass from a standardized survey, and mark-recapture data by sex and year of release and recapture. The details of the model, fits and outcomes are detailed in Mormede et al. (2014a). In the integrated model, natural mortality was assumed known (based on the maximum age of fish caught), movement (post recruitment) was assumed contained within the stock area and approximated using areas-as-fleets, and mark-recapture data were used to estimate absolute annual abundance of the fish population. The Ross Sea region stock was assumed to be closed to immigration and emigration and the spatial stock structure was modelled by allocating fleet effort to three different spatial areas that correspond to different age distributions. Estimates of selectivity in those three spatial areas are shown in Fig. 2 (Fig. 5 of Mormede et al., 2014a). The toothfish tagging program requires all vessels participating in the fishery since 2004 to tag and release one fish per ton caught (Hanchet et al., 2015). Between 2001 and 2017, more than 45 000 toothfish were tagged in the Ross Sea region (Parker and Mormede, 2017a, 2017c).

The integrated assessment model was initialised assuming an equilibrium age structure at an unfished equilibrium biomass, i.e., a constant recruitment assumption. Recruitment sex ratio was assumed to be 50:50 and was parameterised as a year class strength multiplier (assumed to have a mean equal to 1 over a defined range of years), multiplied by an average (unfished) recruitment ( $R_0$ ) and a spawning stock-recruitment relationship. Selectivity for each fishery was parameterised by a sex-based double-normal ogive (i.e., domed selectivity).

Spatial variability in toothfish biological and fisheries parameters through the Ross Sea region were accounted for in the integrated model using three areas-as-fleets. These three components represent the shelf (juveniles), slope (adolescents) and north (spawners). On average, about 1000 toothfish otoliths are used each year to construct two annual area-specific age-length keys for the Ross Sea region (separately for males/females, in two spatial groups: shelf/slope fisheries and north) to produce annual catch-at-age distributions (Parker and Mormede, 2017b).

The model parameters were estimated using Bayesian analysis in two parts. First we maximised an objective function (the maximum posterior distribution or MPD), which is the combination of the likelihoods from the data, prior expectations of the values of those parameters (the prior on initial biomass was set as lognormal and all other priors normal), and penalties (if fish caught or tagged are larger than the fish in the population). Second, we estimated the Bayesian posterior distributions using Monte Carlo Markov Chains (MCMCs). Initial model fits were evaluated at the MPD, by investigating model fits and residuals. Parameter uncertainty was estimated using MCMCs. These

were estimated using a burn-in length of  $5 \times 10^5$  iterations; with every 1000<sup>th</sup> sample taken from the next  $1 \times 10^6$  iterations (i.e. a final sample of length 1000 was taken). The model was fitted to catch proportions-at-age and tag-recapture events i.e., the observed number of fish recaptured with a tag-at-age for each release cohort were fitted to expected values. Following previous recommendations that CPUE indices were not indexing changes in abundance, primarily because the increases in CPUE through time were inconsistent with the expected decrease in biomass due to fishing indicated by other information including mark-recapture data, CPUE indices were not used in the integrated model (Mormede et al., 2014a).

Diagnostic plots of the observed proportions-at-age of the catch versus expected values showed little evidence of inadequate model fit. Estimated selectivity curves appeared reasonable, although the right-hand limb parameters lacked convergence, and is a typical result of spatial patterns in fish size composition combined with interannual differences in the spatial distribution of fishing effort. Post-MCMC analyses of the non-convergence in these parameters showed no evidence that the estimates of initial biomass were unduly influenced. The tag-recapture data were well fitted and provided most of the information on abundance in the model (Mormede et al., 2014a).

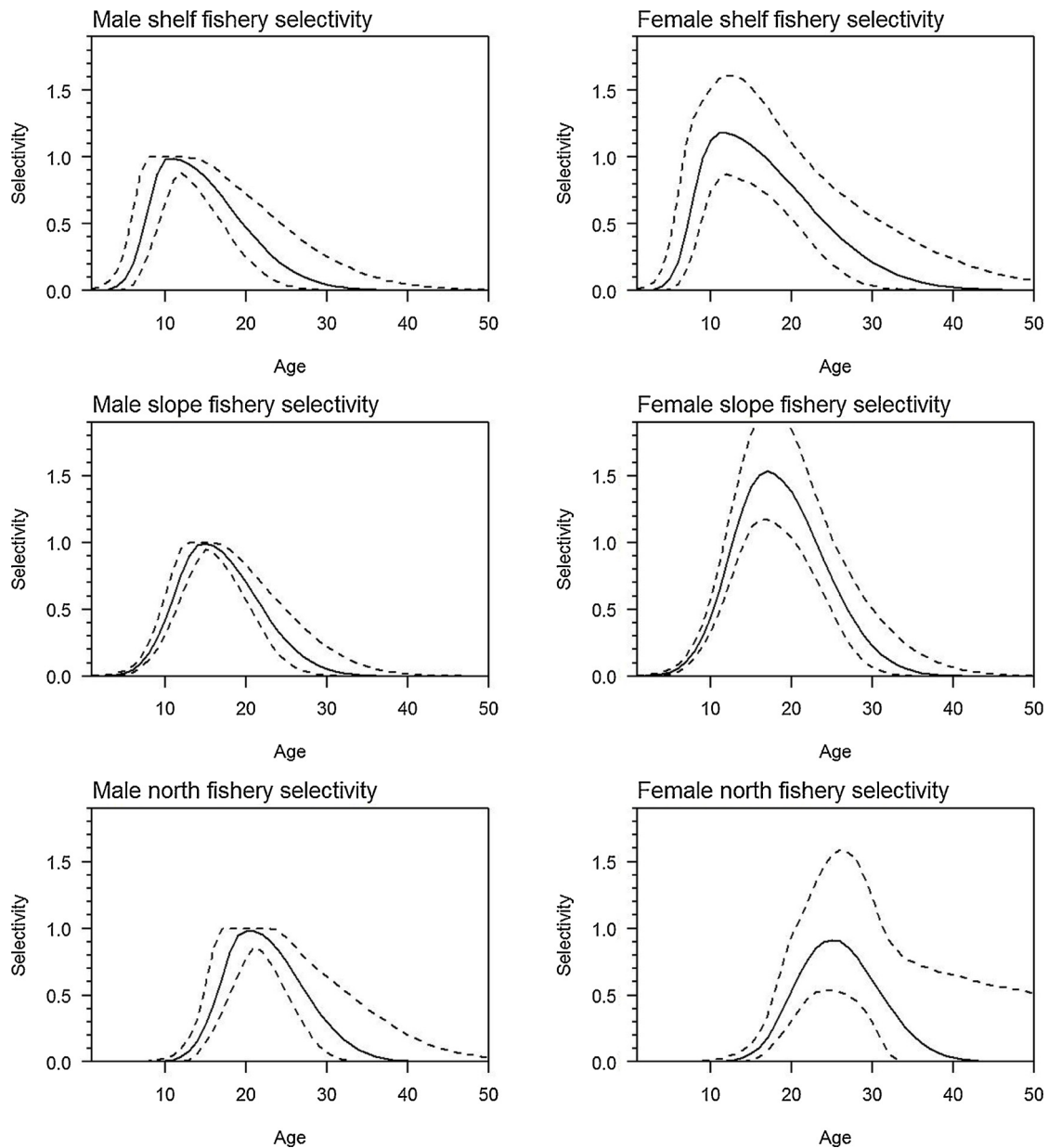
### 2.2.4. Spatially-explicit integrated modelling

A spatially-explicit stock assessment for toothfish in the Ross Sea region was developed using the “Spatial Population Model” software (SPM, Dunn et al., 2012; Mormede et al., 2014b, 2017) to estimate the effect on the integrated stock assessment of ignoring the spatial heterogeneity of the toothfish distribution and spatial heterogeneity in toothfish fishing effort.

Ontogenetic variation in toothfish was represented within SPM using five life history stages: immature, mature, pre-spawning, spawning and post-spawning, with pre- and post-spawning categories used to allow movement of portions of the mature population. The spatial structure of the models was represented by dividing the Ross Sea region into a rectangular grid of 14 rows and 21 columns. Each cell had edges of 156 km, resulting in 189 ocean cells (Fig. 5). The choice of scale was a trade-off between reproducing the required spatial complexity, the available data and computational requirements. Processes were applied to each cell, namely recruitment, spawning, maturation, fishing, natural mortality, and ageing on an annual basis. The population was initialized at an equilibrium state over a 100-year period with no fishing; movement was not permitted in this first phase. In the second initialization phase, for a further 100 years, movement processes were added to the population processes. Movement among cells was parameterized at age separately for juveniles, mature and spawning fish, as estimated preference functions of distance travelled, depth, habitat preference and / or habitat type. Fishing selectivity was assumed constant over the entire domain since availability was explicit within the fish movement. The estimate of selectivity is shown in Fig. 3 (Fig. 5 right of Mormede et al., 2014b). Following initialization, SPM was run with fishing mortality and tagging processes added, based on actual reported catches and tagging rates.

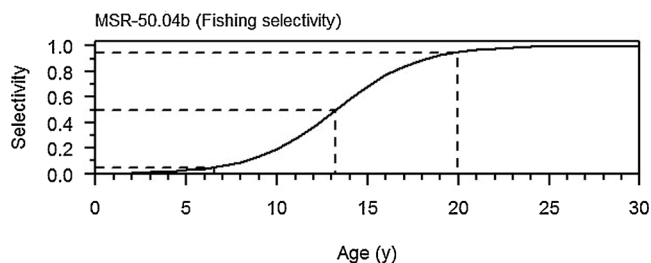
The simulation capability of the SPM model was wrapped into a fully age-based Bayesian framework to allow fitting of movement parameters based on annual age frequencies in each cell, CPUE, and mark-recapture data for both sexes combined. The model was used to investigate the likely bias of using a single-area model (Mormede et al., 2014b), and later to estimate the effects of alternative spatial management scenarios on the stock and the catch limit following the establishment of the Ross Sea region Marine Protected Area (Mormede et al., 2017). The same model was used here as a comparison to the single-area integrated population model and to the spatial distribution modelling using VAST.





**Fig. 2.** Estimated male and female fishing selectivity ogives for the shelf, slope, and north fisheries (solid lines indicate the median and dashed lines indicate the marginal 95% credible intervals) for the single-area integrated stock assessment using CASAL.

Reproduced from Fig. 5 of Mormede et al., 2014a.



**Fig. 3.** Estimated fishing selectivity ogive for the spatially-explicit integrated stock assessment using SPM.

Reproduced from Figs. 5 (right) of Mormede et al., 2014b.

### 2.3. Model comparisons

Results comparing the biomass trajectories through time for the entire stock based on these three models are given, based on the “vulnerable biomass” - the component of the population of toothfish that is accessible to long-line fishing gear used in the Ross Sea region toothfish fishery. We used this measure for comparison because it is the component of the population that is indexed by the catch rates and therefore represented in the VAST results. Vulnerable biomass from the population models was obtained by applying the fishing selectivity to the population structure output from the models (numbers at age times weight at age). The “composite” fishing selectivity for the single-area model with fleet-as-areas was defined as the left-hand limb of the shelf selectivity (juveniles) and the right-hand limb of the north selectivity (spawners). The spatial population model had a single selectivity over the entire domain which was used to calculate the vulnerable biomass.

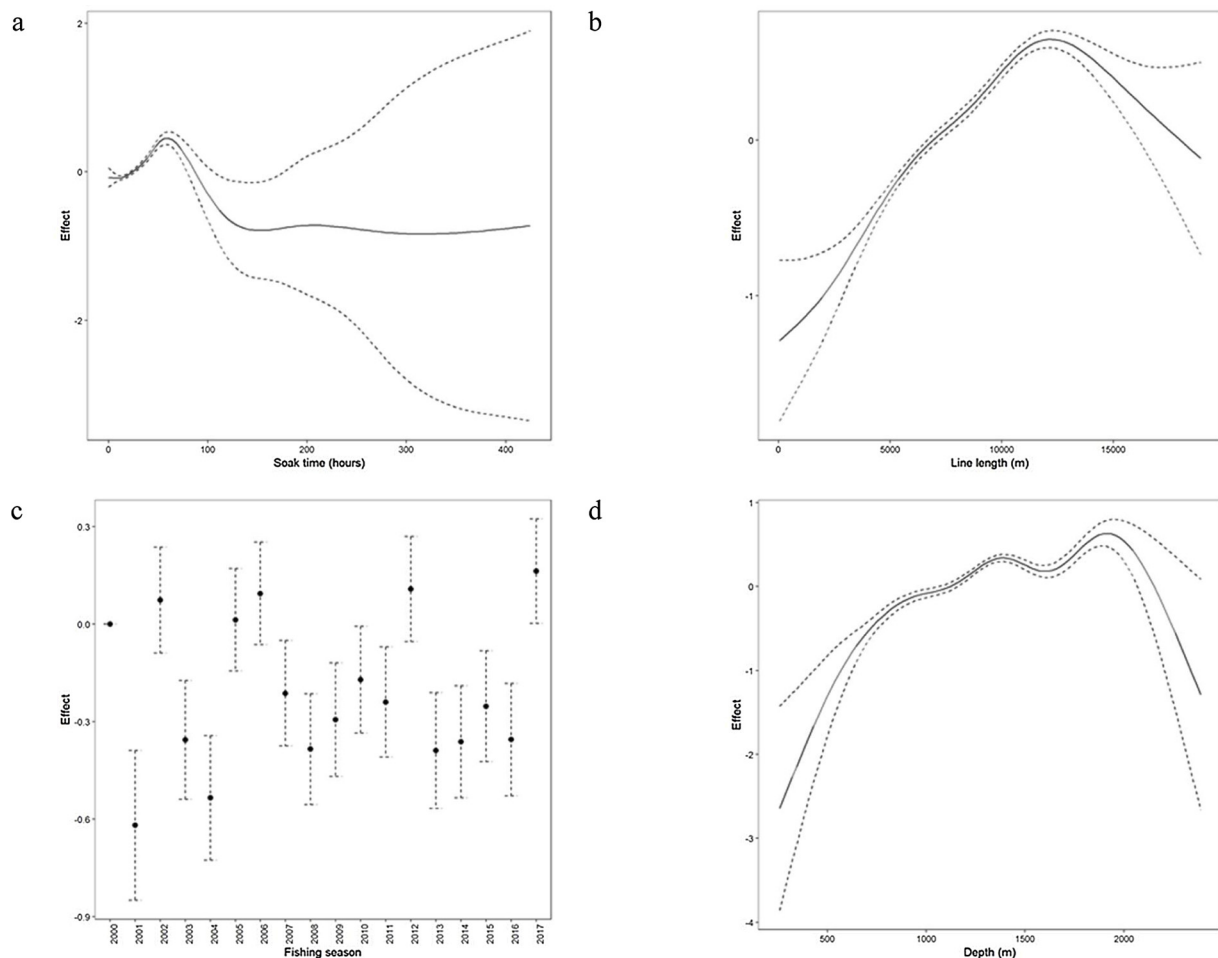


Fig. 4. Parameter effect of the catch per unit effort (CPUE) standardization using GAM (general additive model). a: soak time; b: line length; c: fishing season; d: depth. Dashed lines indicate confidence intervals for the standardizations.

### 3. Results

#### 3.1. CPUE standardization

The significant parameters in the CPUE standardization were vessel, depth, soak time, line length and year (Fig. 4). Catch rates increased almost linearly with depth, soak time and line length to an upper limit where catch rates then decreased or became more uncertain. The standardized catch rates were highly variable among years.

#### 3.2. VAST fitting

We found that for VAST, the best data dispersion model based on AIC value and QQ diagnostic plots was Poisson link for the encounter, and gamma for biomass. There was no strong spatial pattern in the Pearson residuals in the VAST model fits to catch rates: both positive and negative residuals were found on the shelf, slope, and north areas (Fig. 5). Generally, the relative annual biomass trend was insensitive to standardization. The number of cells used in the model or grid type has little influence on the biomass index. The addition of depth and vessel covariates made little difference, whilst soak time changed the absolute biomass trend but not the relative trend. The inclusion of temporal correlation changed the absolute biomass trend and modified the relative trend slightly in 2004 and 2005. Adding the two main bycatch species (grenadier and icefish) did not modify the relative trend in biomass but changed the absolute biomass. The relative annual biomass trend obtained with VAST was very similar to that of the raw and standardized CPUE although the confidence intervals were much

smaller than both the raw and standardized CPUE (Fig. 6).

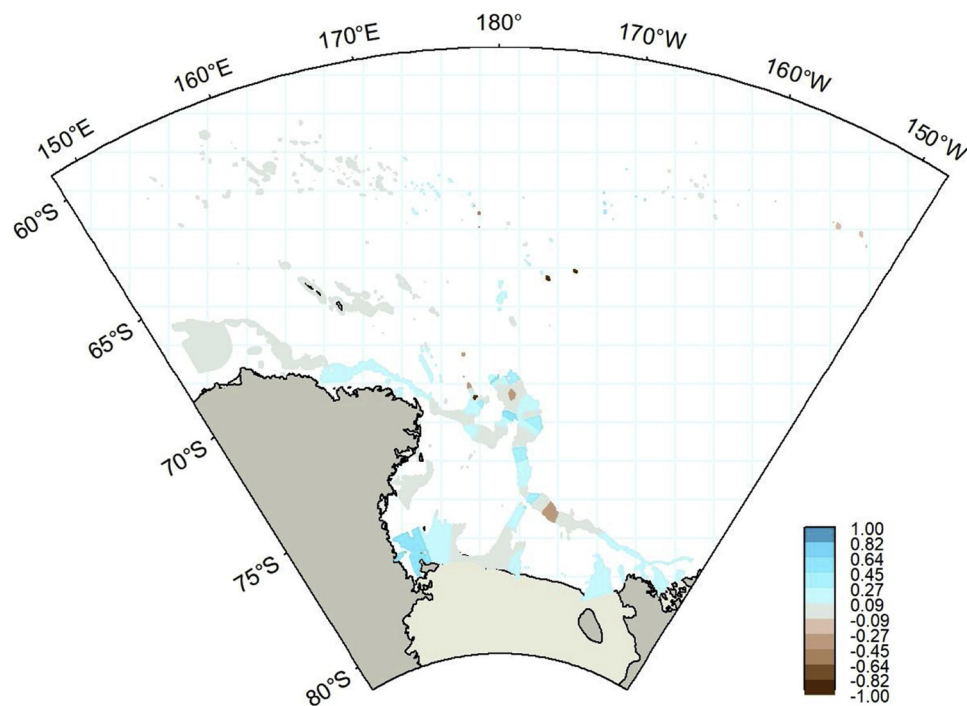
#### 3.3. Comparison of biomass trajectories

##### 3.3.1. Spatial residuals

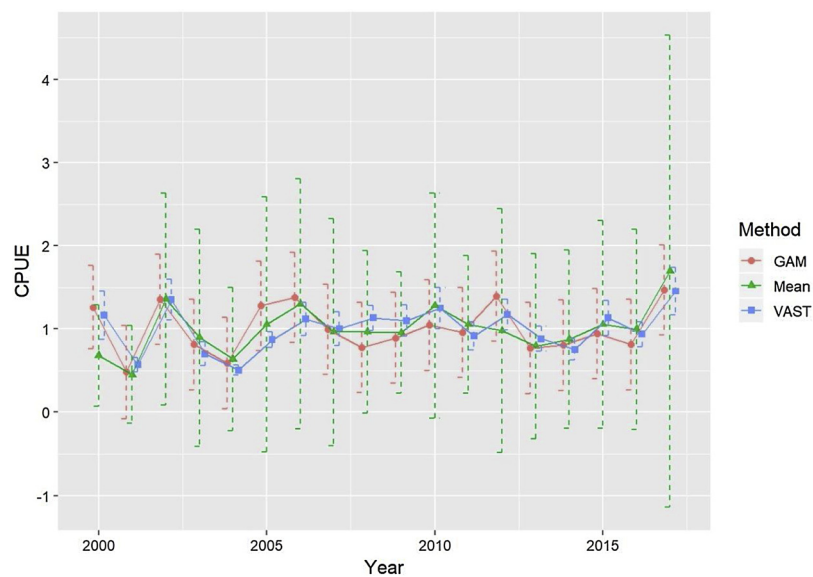
The Pearson residuals to the SPM fits to spatial CPUE were at a coarser spatial scale than that to the VAST model but did not show a coherent spatial pattern, although there were some clusters of cells with only positive or only negative correlations (Fig. 7). These residuals can be compared directly to those in the average residuals from VAST (Fig. 5).

##### 3.3.2. Biomass trajectories

The relative biomass trajectory for both the integrated single-area (CASAL) and spatial (SPM) models shows a slow decline in toothfish biomass over time in the Ross Sea region. The biomass trajectory obtained by VAST is more variable between years and is inconsistent with the biomass trajectory obtained with the integrated population models (Fig. 8). A smoother was applied to the biomass trajectory output from VAST to investigate both the trend and the likelihood of the increases to be consistent with biological parameters. We limited the maximum annual growth rate to 15% in the smoother (i.e., increases could not exceed 15% between successive years), consistent with toothfish natural mortality of 0.13 (Fig. 8) and an assumed closed population. The maximum magnitude of decreases was not constrained in the smoother. The 95% confidence interval around the VAST smoother captured most but not all annual indices.



**Fig. 5.** Median (over the years of the model) catch rate Pearson residuals to the optimized spatial distribution model using VAST. Blue grid shows cells from the Spatial Population Model.



**Fig. 6.** Comparison of the annual CPUE indices from distribution modelling (VAST), CPUE standardization (GAM) or the mean unstandardized annual catch per set.

## 4. Discussion

### 4.1. CPUE standardization and modelling

The biomass trajectory obtained using a standardized CPUE was very similar to the non-standardized (raw) CPUE values and also similar to those obtained using the VAST approach (Fig. 6). The spatial distribution of fishing effort expanded considerably from 1998 to 2005 as more vessels joined the fishery and explorations previously unfished areas of the Ross Sea region were carried out. The spatial distribution of fishing effort is also affected interannual differences in summer sea-ice distribution. The presence of sea-ice can prevent vessels fishing accessing preferred locations. There have also been changes through time to the spatial management of the fishery, for example, the western shelf

was closed to fishing in 2008. Large spatial variations in CPUE are observed in the raw catch-effort data (Hanchet et al., 2015) which means that we would expect CPUE standardization and the VAST modelling to lead to large changes from the raw values CPUE. We should also expect diverging signals between standardized CPUE and VAST models as the CPUE standardization does not account for the change in the location of fishing or fish distribution in space. Factors influencing CPUE have been well studied, and spatial components of both the fish population distribution and fishing patterns in space can lead to hyper-stable or hyper-depleted patterns of CPUE (e.g. Clark, 1982; Hilborn and Walters, 1992). The fact that neither method results in large changes in the pattern suggests that neither is able to properly account for the spatial variability or other factors that influence observed CPUE, even though VAST considers space explicitly.

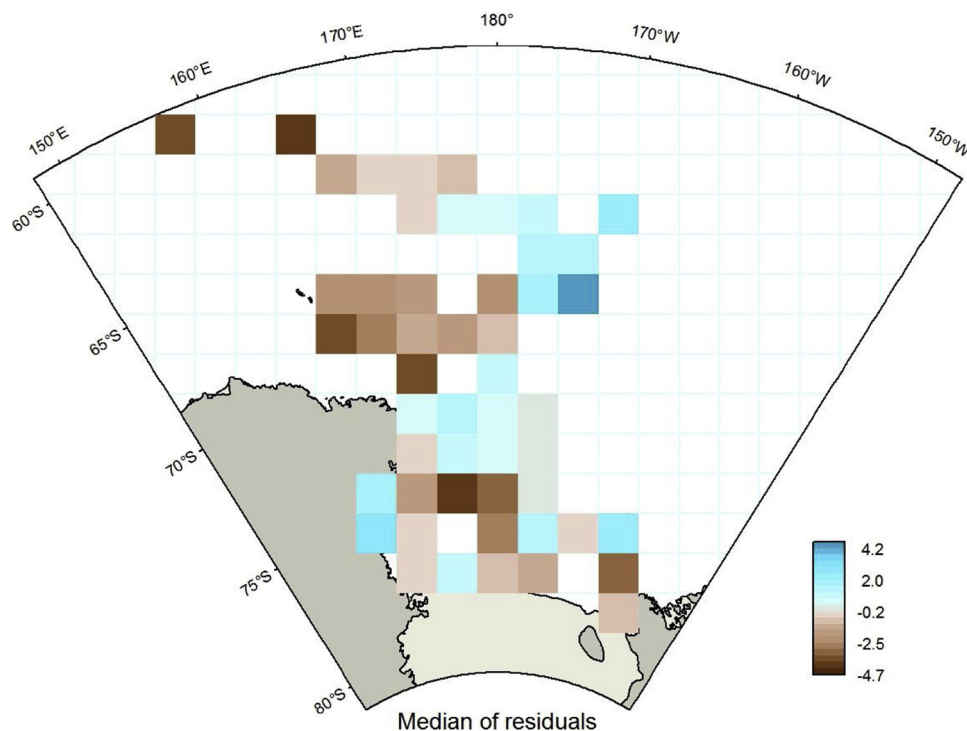


Fig. 7. Median (over the years of the model) Pearson residuals to the fits to the CPUE data for the spatially-explicit integrated population model using SPM.

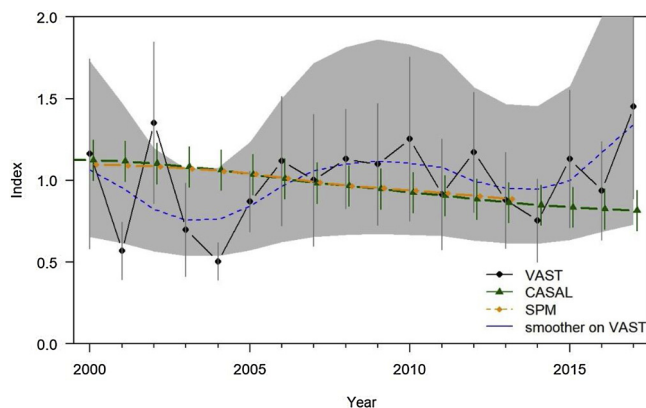


Fig. 8. Comparison of the annual indices from distribution modelling (VAST), single stock population modelling (CASAL) and spatial population modelling (SPM). Also shown is a smoother on the VAST (distribution modelling) index limiting the rate of increase to 15% (blue dotted lines) and 95% confidence interval (grey shading).

#### 4.2. Spatial residuals in distribution

The Pearson residuals to the CPUE data (Figs. 5 and 7) show both a difference in the distribution of the positive or negative residuals, but also four-fold higher residuals for the spatially-explicit integrated model. CPUE data are not generally well fitted in the integrated model, and have been excluded in the Ross Sea integrated model as they were deemed to not represent abundance and therefore conflict with other data in the model (Mormede et al., 2014a).

#### 4.3. Biomass trajectories

The relative trends of the single-area integrated population model and the spatially-explicit integrated population model were nearly identical (Fig. 8). However, their assessment of the absolute differences in toothfish biomass in the Ross Sea region over time differed by

20–35%. Previous analysis comparing the single-area integrated model and the spatially-explicit integrated model have showed the non-spatial population model was likely to underestimate stock size by this amount because it misses (or at least under-represents) toothfish abundance outside the main fishing areas because of imperfect mixing in the population (Mormede et al., 2014b). Essentially, the single-area model estimates the size of the population within the main fishing areas, whilst the spatially-explicit model can account for the biomass over the whole area by inferring biomass outside the fished areas based on fitted habitat associations, where the preference functions are fitted to the data available and the biomass extrapolated to areas unfished.

Both the single-area integrated model and the spatially-explicit integrated model showed a slow decline in biomass, consistent with the expected effects of fishing on the stock. The main information driving those models are the size of fishery removals (catches), mark-recapture data, and biological parameters provided to the model to estimate initial population biomass.

The biomass trajectory obtained using VAST was highly variable through time and inconsistent with the trends obtained using the single-area integrated population model or the spatially-explicit integrated population model. Furthermore, the interannual variability observed in the biomass trajectory using standardized CPUE or VAST were inconsistent with biological parameters of toothfish, which indicate that interannual increases in population biomass should not exceed 15%, unless there is net immigration (Fig. 8). Annually-varying immigration and emigration of toothfish from the Ross Sea region of the level required to explain these large fluctuations is unlikely given the low movement rates for individuals observed from tag release-recapture data (Hanchet et al., 2015).

We note that VAST has been successful in the analysis of survey data to investigate long-term biomass changes, including when using fishery-dependent data rather than survey data (e.g. Thorson et al., 2016; Thorson and Haltuch, 2018). However, in the present study, it seems that VAST was not able to correct for the high spatial variability in commercial catch rates to obtain the underlying spatial distribution of toothfish or to provide reliable information on changes in stock abundance through time. Even though the population models (using



CASAL or SPM) are likely to be biased, they indicate a likely trajectory for the population consistent with the effects of fishing expected for this population, which is not captured at all by the VAST models. It is possible that changes in fisher behavior that influence CPUE, and the low level of mixing within the toothfish population confound approaches to using CPUE as an index of stock abundance in the Ross Sea region toothfish fishery. Certainly, the caveats surrounding CPUE as an index of abundance at large spatial scales (e.g. Prince and Hilborn, 1998) will be more important when fishery catch data are used compared to when fishery survey data are used because of issues of variable fishing methods, targeting, and variations in the spatial distribution of fishing through time. Fisheries catch rates are likely to be hyper-stable (Harley et al., 2001; Maunder et al., 2006) and typically not representative of the underlying biomass. In this regard, the biomass trajectories obtained using spatial modelling methods including VAST were inconsistent with the expected trajectory of this population in the initial “fish-down” phase. The spatial standardization using VAST was insufficient to allow CPUE to index changes to toothfish abundance in the Ross Sea region (Hanchet et al., 2015).

## 5. Conclusions

Although it has been successful in other instances (e.g., Thorson et al., 2016), we found that spatial distribution modelling was not able to standardize for fisher targeting areas of higher CPUE, even when the models were run at a very fine spatial scale. We conclude that distribution models based on CPUE information from the fishery (rather than research fishery surveys) and which do not include biological processes should be used with caution to obtain biomass trajectories, particularly in instances where the CPUE is not expected to be an index of abundance. Adding biological and fisheries processes within distribution models could help inform research and management where data or resources are insufficient to build fully spatially explicit stock assessments. Variations between years from purely statistical models should be compared with process-based expectations of stock dynamics, including the relative magnitudes of annual stock productivity, immigration/emigration, and biomass removals by the fishery.

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