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Using spatial population models to investigate the potential effects of the Ross Sea region Marine Protected Area on the Antarctic toothfish population

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ABSTRACT

One aim of Marine Protected Areas (MPAs) is to protect a representative portion of the environment through spatial closures to extractive practices such as fisheries. Although they usually involve the displacement of fisheries, their design rarely takes into account the effect of displacing that fishery on the target fish population. We used a spatially explicit population model of Antarctic toothfish in the Ross Sea region to investigate the effects of the endorsed Ross Sea region MPA on the fishery dynamics and the spatial distribution of the toothfish population. Our study indicates that the MPA will likely improve protection of the juvenile population residing on the Antarctic Shelf, while the number of areas with high levels of depletion is unlikely to increase compared to status quo management. Results also suggested a small increase in the catch limit under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) harvest management rules, but with a slight reduction in catch rates. We have showed that spatial modelling tools can help inform MPA planning by simultaneously quantifying potential effects on the fish population and the ability to achieve conservation goals.

1. Introduction

Marine Protected Areas (MPAs) are increasingly used as a tool to conserve, manage and protect the oceans. Traditionally, MPAs aimed to eliminate potential threats to parts of the ecosystem in particular locations or to protect a representative portion of particular habitats, by implementing spatial prohibitions on extractive practices such as fisheries (IUCN, 2013). However their aims have diversified, and can include enhancing benefits to the fishery they are applied to (e.g., Brown, 2016; Gruss, 2014; Rassweiler et al., 2012). MPAs can be designed by optimising the size and location of these spatial closures based on the specific protection objectives of the MPA and taking into account the cost of the changes to extractive and other practices (see syntheses in, for example, Crowder and Norse, 2008; Ehler and Douvere, 2009; Groves et al., 2002; Leslie, 2005).

Spatial analyses are required to understand the biological and financial implications of such closures (Sanchirico 1999). The effects of proposed spatial closures and other spatial management options on fleet behaviour and their financial returns have been studied (Bastardie et al., 2014; Holland, 2000; Lehuta et al., 2013). Results from these studies showed that the design of each proposed MPA had strong impacts on its effectiveness to protect species as well as on the cost to the fishery, and could be either positive or negative. Furthermore, accurately anticipating the consequences of alternate proposed spatial management scenarios on the fish populations requires understanding the spatial demographics, movement patterns, and dynamics of impacted populations as well as the fleet behaviour at the scale of the proposed spatial management or smaller (Botsford et al., 1993; Christensen et al., 2009).

Studies investigating the potential impact of MPAs on the ability to accurately estimate biomass within stock assessment models have shown that MPAs could result in a bias in the estimation of the fish population, particularly for larger MPAs, if data are not available inside the MPA or if a single area model is used averaging processes inside and outside the MPA (McGillard et al., 2014; Pincin

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Table 1
Biological parameters used for Antarctic toothfish in the model.

Relationship	Parameter	Value
Natural mortality	M (y^{-1})	0.13
Von Bertalanffy growth curve	t_0 (y)	−0.117
	k (y^{-1})	0.091
	L_∞ (cm)	174.5
	c.v.	0.1
Length-weight regression	a	$1.051e^{-08}$
	b	3.036
	c.v.	0.1
Maturity	a_{50} ($\pm ato_{95}$)	12.2 (±2.8)
Stock recruit steepness (Beverton-Holt)	h	0.75
Recruitment variability	σ_R	0.6
Ageing error (CV)	c.v.	0.1
Initial tagging mortality	(%)	10
Initial tag loss (per tag)	(%)	3.3
Instantaneous tag loss rate (per tag)	(y^{-1})	0.062
Tag detection rate	(%)	98.8
Tag related growth retardation	(y)	0.5

Table 2
Depletion level of the total biomass in 2048 as a proportion of the unfished biomass in 1995 ($1 - B_{2048}/B_0$) and mean fish age at the start of the fishery (at B_0) and in 2048 (at B_{2048}) for each zone.

Metric	Scenario	Shelf	Slope	North
Depletion in 2048 ($1- B_{2048}/B_0$)	1. Status quo	0.28	0.40	0.47
	2. MPA and historic distribution	0.23	0.40	0.51
	3. MPA and spreading distribution	0.23	0.40	0.51
	4. Proportional to vulnerable biomass	0.26	0.39	0.49
Mean age at B_0		6.6	10.3	17.7
	1. Status quo	6.0	8.6	15.3
	2. MPA and historic distribution	6.1	8.6	15.0
	3. MPA and spreading distribution	6.1	8.6	15.0
Mean age at B_{2048}	4. Proportional to vulnerable biomass	6.0	8.7	15.1

and Wilberg, 2012; Punt et al., 2016). Spatial population models have also been used to investigate the likely impacts of alternate spatial fisheries management scenarios on fish populations as part of MPA design (e.g., Colloca et al., 2015; Edwards and Plagányi, 2011; Metcalfe et al., 2015), showing that specific portions of the fish populations (either juveniles or lager older fish) need to be protected for the MPA to achieve an ecosystem conservation goal. However, limitations of current modelling approaches to provide useful advice include the spatial scale at which fish movement is often modelled (e.g., Bastardie et al., 2014; Lehuta et al., 2013), and the fact that displacement of fishery effort is often not included in these models, therefore ignoring increased effort and associated negative impacts on other parts of the ecosystem (see Gruss, 2014 for a review).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the international body which manages the conservation and rational use of Antarctic Marine Living Resources, including Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. Spatial management is carried out through a network of open and closed areas, whereby the closed areas are designed to protect target and by-catch species from the effects of fishing (Conservation Measure 32-02 CCAMLR-XXIV, 2015; Hanchet et al., 2015b). These open and closed areas were initially set arbitrarily circumpolar to protect a proportion of the ecosystem prior to fishing, and have been modified through time as knowledge of the ecosystem has increased. In October 2016, CCAMLR established the Ross Sea region Marine Protected Area (RSR MPA), the first of its kind in international waters (CCAMLR, 2016), following scientific advice. The RSR MPA was designed to protect the biodiversity of the Ross Sea region. One of its objectives is to protect areas of importance in the life cycle of Antarctic toothfish, with all other objectives centred on other ecosystem functions.

The fishery for Antarctic toothfish in the Ross Sea region started in 1997, expanding to taking the catch limit from 2005 onwards. The population size of Antarctic toothfish in the Ross Sea region has been assessed using a single area stock assessment (Mormede et al., 2014a). This stock assessment and subsequent updates are used to set the catch limit in the Ross Sea region. In 2015, the spawning stock biomass was at 70% of unfished spawning stock biomass (30% depletion), i.e. this stock is still in a fishing-down phase (CCAMLR, 2015). A spatial population model of toothfish was developed for the Ross Sea region to investigate the potential bias of the single area stock assessment that ignores the spatial structure of the population and the fishery (Mormede et al., 2014b). Results showed that the single area model was likely to under-estimate the biomass of the stock by 30–50%.

This study aims to investigate the effects of the redistribution of the location of catches of toothfish on both the toothfish population and its fishery due to the inception of the RSR MPA. We use the spatial model developed by Mormede et al. (2014b) and apply spatial management simulations reflecting the RSR MPA design. We investigate the effects of the corresponding fishing displacement scenarios on the toothfish population, whether localised depletion will occur in the Ross Sea region as well as its degree and location, along with alternate effort displacement scenarios. We also quantify the effect that the MPA might be expected to have on the catch limit and catch rates under current CCAMLR harvest management rules.

2. Methods

2.1. Antarctic toothfish in the Ross Sea region

Antarctic toothfish are a large nothotenoid fish found around the Antarctic continent. They are closely related to Patagonian toothfish (*Dissostichus eleginoides*), but generally found at lower latitudes than Patagonian toothfish which lacks anti-freeze protein. Patagonian toothfish are caught in small numbers in the northern part of the Ross Sea region and are not included in this analysis. Antarctic toothfish mature at about 10 years of age for males and 15 years for females (50% maturity) and grow to a maximum size of 1.8 m at about 35 years of age (Hanchet et al., 2015a; Parker and Grimes, 2010). Biological parameters for Antarctic toothfish are summarised in Table 1. In the Ross Sea region, Antarctic toothfish are a top predator, with stable isotope levels of carbon and nitrogen (δ15N and δ13C) similar to that of Weddell seals and killer whales (Pinkerton et al., 2010). They are expected to have a moderate trophic importance in the Ross Sea foodweb whereby changes to the toothfish population are unlikely to cascade through the ecosystem by direct trophic effects (Pinkerton and Bradford-Grieve, 2014). However, Antarctic toothfish might be an important part of the diet of other top predators at specific times of the year such as Weddell Seals during lactation and post-lactation recovery periods (Eisert et al., 2013). As such, it is important to understand the impacts of any new management regime on expected toothfish population distribution and trajectories given the potential ecosystem impacts it may cause throughout the Antarctic Ocean.

The Ross Sea region is likely to comprise an enclosed unit stock of Antarctic toothfish, centred on the Ross Sea gyre. The life cycle

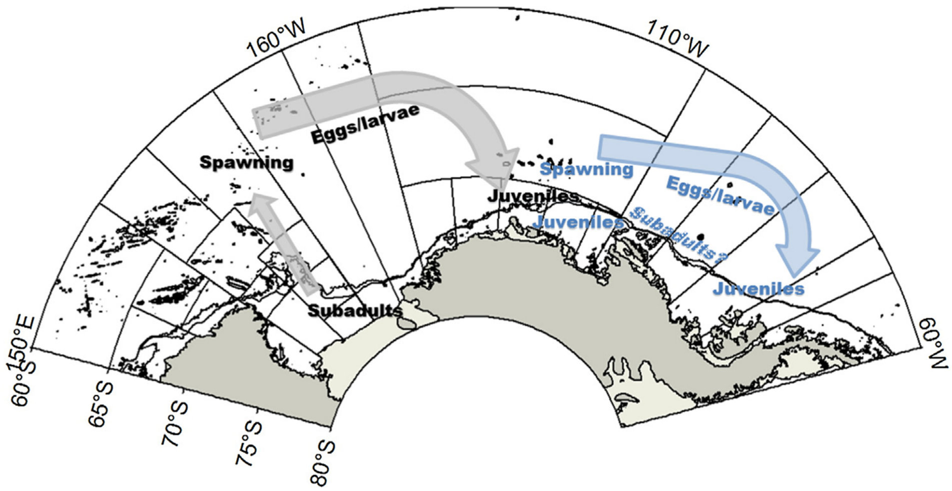

Fig. 1. Hypothesized biological structure for Antarctic toothfish stocks in the Ross Sea region (black text and grey arrows) and Amundsen Sea region (blue text and arrows). Eggs/larvae (<30 cm), juveniles (30–80 cm), subadults (80–120 cm), spawning (>120 cm). Italics indicate uncertain distribution (Fig. 10 from Parker et al., 2014). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of Antarctic toothfish in the Ross Sea region largely consists of juveniles and young adult fish recruiting to the Ross Sea shelf, progressively moving deeper as they mature to the slope where most adults are found, and migrating to seamounts in the north of the Ross Sea region to spawn (Fig. 1). The eggs and larvae are then transported back to the shelf by the Ross Sea gyre (Hanchet et al., 2008, 2010). This progression is evident in the mean age of fish in each of these zones for example (Table 2).

2.2. Spatially explicit population model

We used the SPM (Spatial Population Model) platform to carry out the simulations (Dunn et al., 2012). Spatially explicit models of Antarctic toothfish have been developed for the Ross Sea region (Mormede et al., 2014b). These are fully Bayesian age-based single sex models extending the full Ross Sea region, from 155°E to 170°W and 60°S to the shelf edge at approximately 78°S. The region is divided in 189 equal area cells with side lengths of 156 km. The models are limited to the 120 equal area cells (24 000 km^2) where at least 5% of the cell contained depths deemed suitable toothfish habitat (450 m to 2870 m based on Gebco depth locations where 95% of the fishing has occurred); all cells excluded from the model are assumed to contain no toothfish. This spatial extent was tested and showed to be the most appropriate at the time (Mormede et al., 2014b). The spatial models were fitted to fishery data available from CCAMLR. Although no fishery-independent data were included in the model, all vessels fishing in the Ross Sea region are required to have two scientific observers on board (one national and one international CCAMLR scientific observer) and follow a comprehensive data collection protocol. The data included in the models were year- and cell-specific catches, catch rates, proportion mature at age, age frequency, and mark-recapture data. Table 1 summarises the biological parameters and Fig. 2 the movement processes in the model. The selected model estimated 34 parameters: 4 maturation and spawning parameters, 3 fishing selectivity parameters, 3 tagging selectivity parameters, and 24 movement parameters. The unfished biomass distribution in space for immature, mature and spawning toothfish is presented in Fig. 3. Investigations showed that the total unfished biomass was poorly estimated when movement was estimated concurrently. Therefore, the unfished biomass was not estimated in this model but fixed at the value of the single area stock assessment (Mormede et al., 2014a).

The SPM framework allows for movement between cells to be parameterised as either discrete (individually estimable between cells), following an estimable diffusive process, or as a probability function of attributes, distance, and/or density, which can be time varying. In this model, each movement process was parameterised as a probability density function based on attributes of that location, and the distance from their previous location. Here, we define the preference for each spatial attribute $A_i(x)$ in each cell x as the function $f_i(\theta_i, A_i(x))$, where θ_i are the parameters for the function f_i (of user-defined functional form). Each spatial attribute $A_i(x)$ can be time varying. Given a set of n attributes for the domain, we can define the aggregated or total preference function for each individual cell x in the model as the weighted product of individual preference functions,

$$P_x = f_1(\theta_1, A_1(x))^{\alpha_1} \times f_2(\theta_2, A_2(x))^{\alpha_2} \times \ldots \times f_n(\theta_n, A_n(x))^{\alpha_n}$$

where α_i is an estimated weighting factor for each attribute $A_i(x)$. At least one α_i is fixed to the value of one to avoid over-parameterisation. Then for each cell 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), as the ratio of the preference of being in cell a to the sum of the preference in all the cells.

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

The movement of juvenile, mature and spawning fish was estimated by the spatial estimation model of Mormede et al. (2014b) through three separate preference functions based on environmental variables and distance travelled. The movement from each cell within each of those groups was constant by age and through time, i.e. all juvenile fish behaved in the same manner regardless of age or year differently depending on their location (as distance travelled is an attribute used). All movement parameters were estimated within the model by fitting the model to fishery. The environmental variables retained through model selection were depth, suitable habitat and whether the cell contained hills or not.

Simpler models were also constructed out to test simpler hypotheses than the expected ontogenetic movement of fish and spawning migration. These models tested for the likelihood of a simple movement of fish as a function of distance or the distribution of recruits throughout the domain rather than limited to the

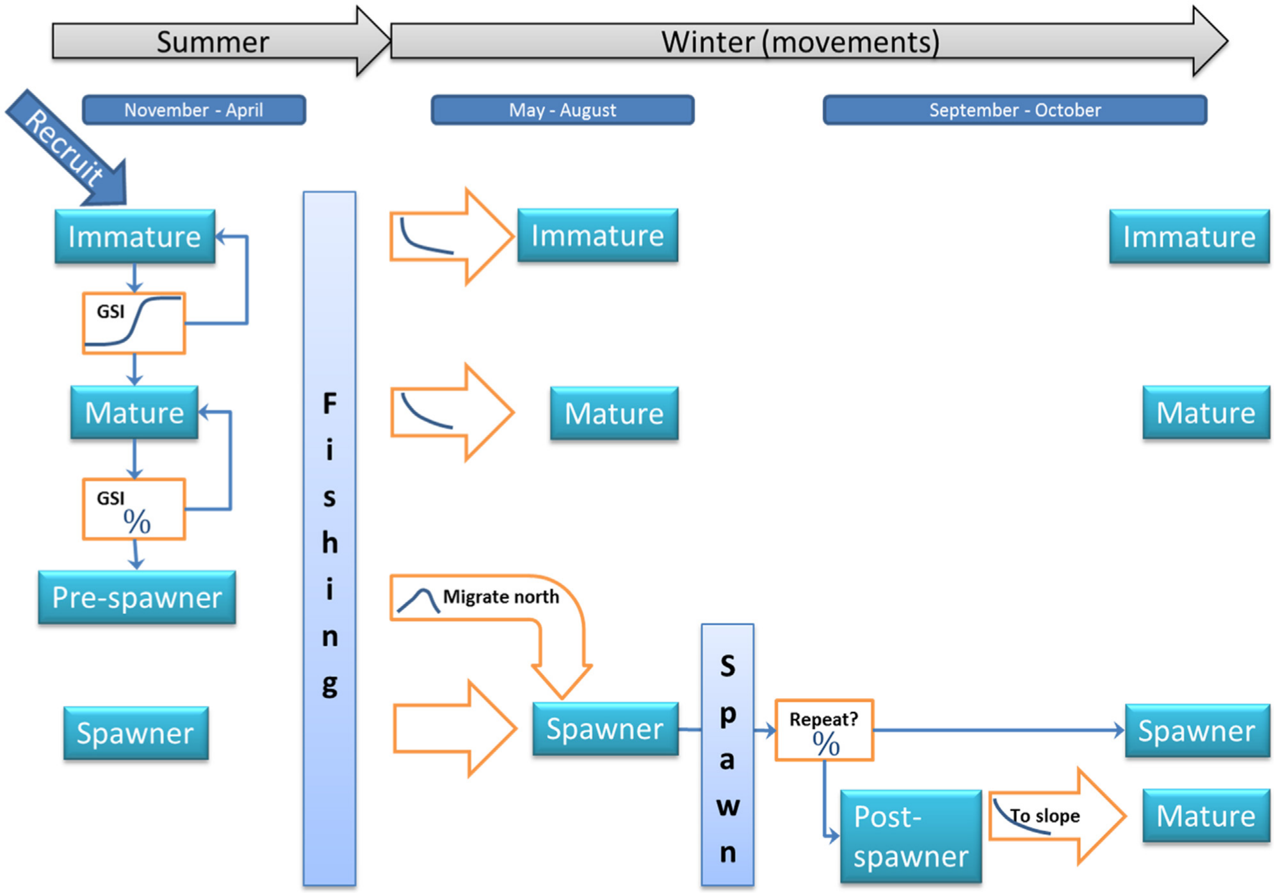

Fig. 2. Proposed life history of Antarctic toothfish in the Ross Sea region as applied to the model. Arrows indicate inferred movement of that fish category, where appropriate via an ogive. Boxes indicate a transition between fish categories, where appropriate via an ogive.

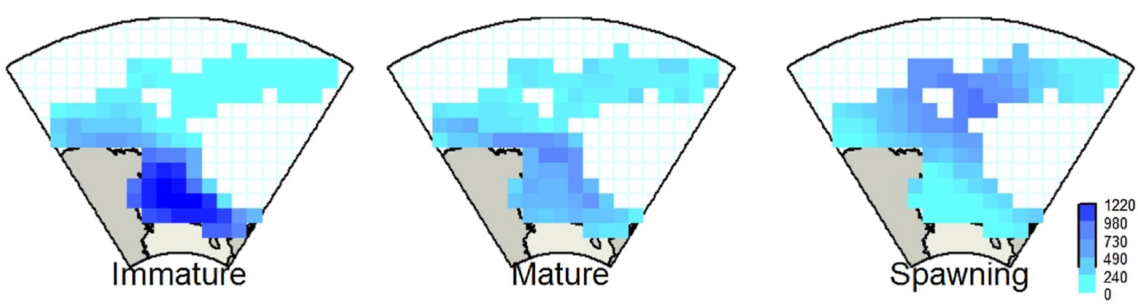

Fig. 3. Distribution of initial total biomass (in thousands of tonnes) for immature, mature and spawning toothfish as estimated by the spatial model developed by Mormede et al. (2014b). Only cells with positive biomass are presented (cells in white are excluded from the model because they are too deep for toothfish).

areas shallower than 800 m depth, or the lack of spawning migration whereby mature fish can spawn everywhere. All these models provided poorer fits to the data than the more realistic models described above, with a reduction of between 10 and 20 parameters estimated, yet an increase in the objective function by over 1000 points in every case.

The selected model describes the generalised spatial distribution and ontogenetic movement of toothfish in the Ross Sea region relatively well, as evidenced by the spatial fits to age data, catch rates, spawning status, and tag recoveries (Mormede et al., 2014b). That this model does not capture small scale anomalies such as the presence of very large toothfish in McMurdo Sound on the very shelf edge in shallow waters where only small toothfish were expected by the model (Parker et al., 2016). This is unsurprising because of the spatial resolution of the model (cell size 24 000 km^2) and the generic way it handles movement as a function of average environmental conditions prevailing across entire cells. The optimised model described above was developed by Mormede et al. (2014b) and used here as a simulation platform.

2.2. Choice of scenarios

The catch limit for Antarctic toothfish in the Ross Sea region was set at 3044 t for the 2013 and 2014 fishing seasons based on the results of the 2013 stock assessment (Mormede et al., 2014a). This catch limit is split into three regional catch limits for the shelf,

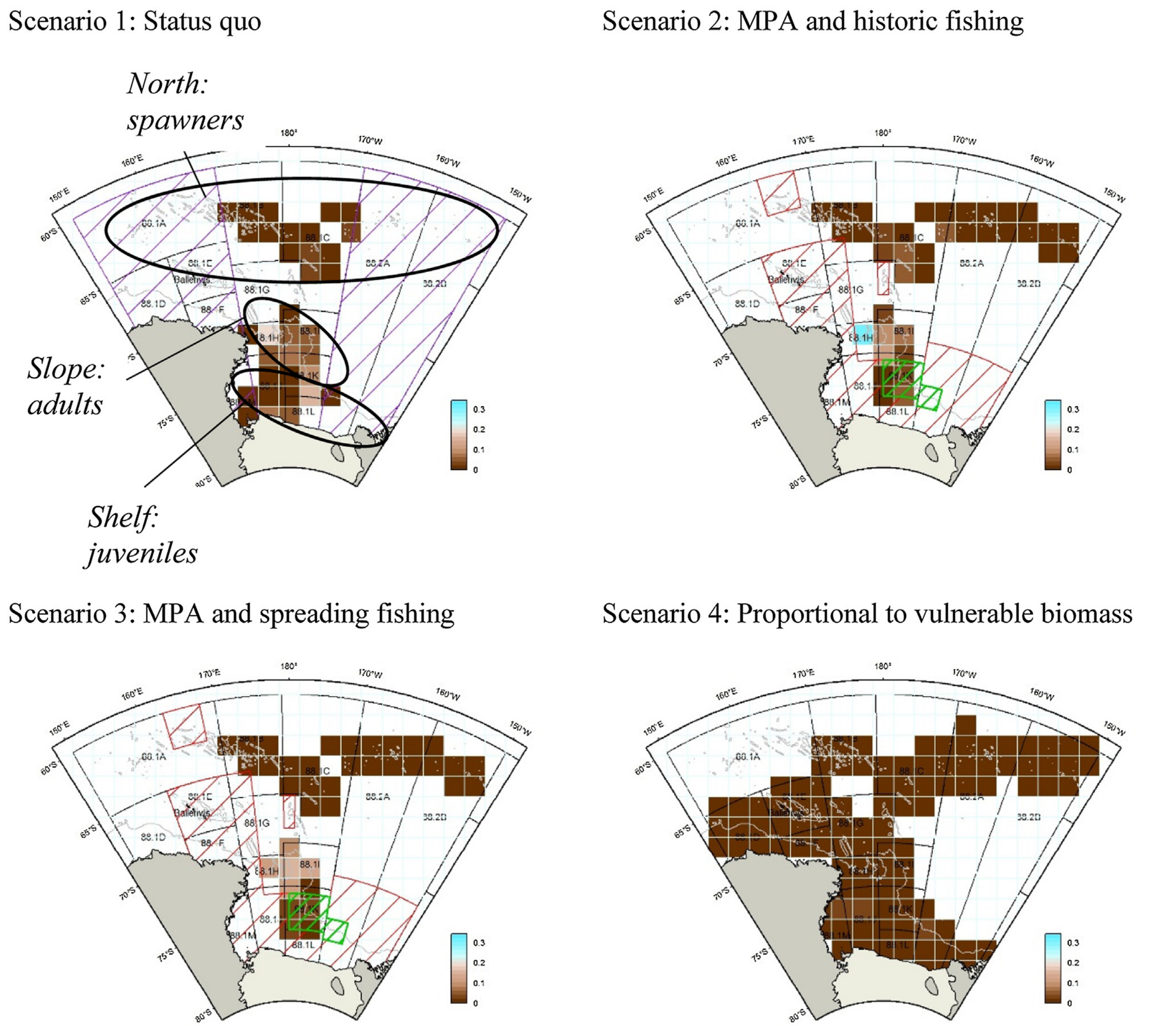

Fig. 4. Spatial distribution of annual constant future catches under four alternate scenarios over the 35 year projection; each cell is expressed as a proportion of the total catch per year. Only cells with positive catch are presented (cells with zero catch are in white). Location of the shelf, slope and north zones are depicted in the top left panel. The locations closed to fishing through current management decisions are depicted in purple hash (top left panel), by implementation of the RSR MPA are depicted in red hash; the Special Research Zone is depicted in green hash. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

slope, and north zones of the Ross Sea region (shown in the top left panel of Fig. 4). Large portions of each of these zones within the Ross Sea region are currently closed to fishing (see Fig. 1 in Hanchet et al., 2015b and top left panel of Fig. 1), although these do not have MPA status.

In this study, we projected the optimised spatially explicit population model 35 years from 2014 to 2048 using various scenarios of future spatial catch distributions. For each scenario, the future catch level and distribution was constant over the 35 year projection. The spatial distribution of catch for each scenario was set as discussed below, and the total constant annual catch for each scenario was set to achieve the CCAMLR management rule which dictates that the spawning stock biomass in 2048 reaches $SSB_{50\%}$ (50% of its unfished level over the entire Ross Sea region) under CCAMLR harvest management rules. The areas open or closed to fishing (through the MPA or some other management measure) and the resulting spatial distribution of catches under each scenario are depicted in Fig. 4.

The RSR MPA is complex: it includes areas closed to fishing (including some areas previously open), areas open to fishing (including some areas previously closed), and an area with lim-

Table 3
Summary of the distribution of constant future catches per zone for each of the scenarios over the 2014–2048 projection period. Note that the shelf area includes the Special Research Zone (SRZ).

Scenario	Shelf	Slope	North
1: Status quo	0.40	0.46	0.14
2: MPA and historic distribution (10% in SRZ)	0.14	0.55	0.30
3: MPA and spreading distribution (10% in SRZ)	0.16	0.54	0.30
4: Proportional to vulnerable biomass	0.37	0.33	0.30

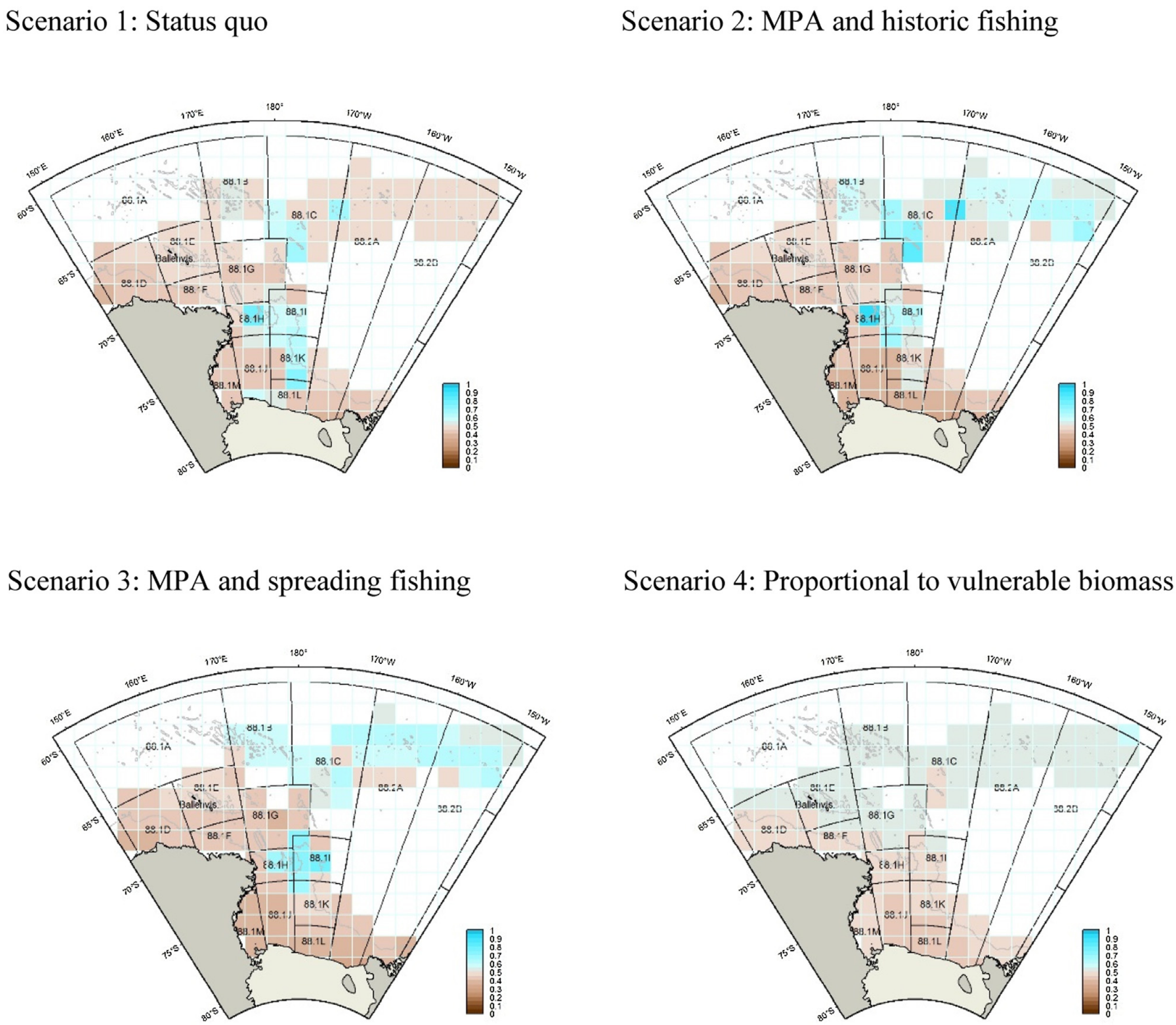

Fig. 5. Index of depletion levels of each cell in 2048 as a proportion of the total unfished biomass. Only cells with positive biomass are presented (cells in white are excluded from the model because they are too deep for toothfish).

Table 4
Summary of results for the different scenarios. All biomasses referred are in total biomass, and depletion calculated to 2048 (35 years from the start of simulations).

Scenario	0. Status in 2013	1. Status quo	2. MPA and historic fishing	3. MPA and spreading fishing	4. Proportional to vulnerable biomass
catch limit (% change from scenario 1)	–	–	+6.0	+4.2	+1.7
Total catch caught in excess of that of scenario 1 over 35 years (assuming the catch limit is caught, in t)	–	–	+5 460	+3 780	+1 540
Depletion level of the most depleted cell $(1- B_{2048}/B_0)$	0.39	0.66	0.84	0.68	0.54
Of least number of cells collectively containing 80% of unfished total biomass, percentage with depletion < 0.25 depletion < 0.75	20 0	12 0	38 2	40 0	11 0
Gini index	0.32	0.36	0.37	0.37	0.37
D80 (number of cells)	59	56	54	55	55
Catch rate in 2048 (kg per thousand hooks)	479 (in 2013)	392	336	323	306
Catch rate in 2048 relative to scenario 1 (%)	122	100	86	82	78

ited fishing allowed, called the Special Research Zone (SRZ). The RSR MPA, including the SRZ, is depicted in Fig. 4, in scenarios 2 and 3. Under the existing CCAMLR harvest management rule of $SSB_{50\%}$ in 2048, the MPA will displace fishing effort away from the areas closed to fishing within the MPA and into other areas open for fishing. Catch limits in the future will continue to be set by applying the CCAMLR harvest management rules through a stock assessment process, including setting the catch limit which achieves a reduction of the spawning stock biomass to $SSB_{50\%}$ (50% of its unfished biomass at the stock level) within 35 years. In this simulation the catch limits were simply scaled to achieve $SSB_{50\%}$; the full stock assessment is not carried out. The regional split in the catch limit between the shelf, slope, and north zones of the Ross Sea region used for the 35-year model projections are detailed in Table 3. 30% of the total catch is allocated to the north based on expected vulnerable biomass distributions between the areas open to fishing under the MPA scenario (Delegation of the USA and Delegation of New Zealand, 2013). The RSR MPA agreement has set an initial temporary limit of 19% based on international consensus; this limit is to be reviewed with scientific advice after the MPA has been in place for a couple years and further data are available to provide further scientific advice (CCAMLR, 2016).

The spatial behaviour of the fishing fleet is mostly affected by catch rates, the areas open or closed to fishing, ice cover, and the catch limits in each zone. The distribution of catches has been relatively constant over the last 5–10 years of the fishery, whereby fishing has been concentrating on the grounds with higher catch rates but also those that are accessible year after year with little gear loss for example. Effects such as distance from port, fish price, and fuel price have a limited impact on fleet distribution since the fishing grounds are so far away from port and the fishery is a single-species fishery. Therefore the projected catch distribution for years 2014–2048 was assumed constant rather than modelled using individual-based models as has been done elsewhere (e.g., Bastardie et al., 2014). The resulting catch rates in 2048 were calculated for the different scenarios, as these are a driver of fishing behaviour and a likely cost of MPAs, but in this instance is dampened by sea ice conditions and local catch limits. Catch rates were calculated in each scenario by multiplying the selected biomass in each cell in 2048 with the catchability estimated by Mormede et al. (2014b) and reported as a catch-weighted value of that catch rate for the entire Ross Sea region.

Scenario 1 assumes the management of the fishery in the Ross Sea region continues under the current regime of open and closed areas and a continuation of the currently established fishery. Under this scenario we assumed that the spatial distribution of future catches will approximate the average distribution between 2009 and 2013, and that the catch limit remains unchanged (as it currently satisfies the CCAMLR management rule). The years 2009–2013 were chosen as they represent a time with stable spatial management (other areas were open to fishing prior to this time) as well as a stable effort distribution and total catch per year.

Scenarios 2 and 3 assume that management in 2014 is modified consistent with the implementation of the RSR MPA (this MPA will come into effect on 1st December 2017 and not in 2014). The MPA assigns a specific lower proportion of the catch (10%) to the special research zone (SRZ) as an area “lightly fished” to compare and contrast in the future; with the rest of the catch distributed to the remaining areas of the shelf, the slope and north as in Table 1. The difference between these two scenarios lies in the relative distribution of catch between the different cells which are open to fishing; the relative catch in the SRZ remains constant at 10% of the total catch.

In scenario 2 we assume that fishers will continue to fish in their preferred locations rather than spend time exploring new areas as this is an Olympic fishery (fishing ceases as soon as the catch limit is reached by the fleet; there is no allocation by vessel). In cells previously fished, the catch assigned is the average observed catch from 2009 to 2013. In cells not previously fished, the catch assigned is the average observed catch from 2009 to 2013 of the nearest cells which have been fished. Furthermore, in order to satisfy the $SSB_{50\%}$ CCAMLR harvest management rule, these catches are then scaled up or down to insure that the total spawning stock biomass is at 50% of unfished spawning stock biomass by 2048 ($SSB_{2048} = SSB_{50\%}$); the sum of the catch in all the cells forms the annual catch limit (constant over the next 35 years).

In scenario 3, we again assume that management in 2014 is modified consistent with the implementation of the RSR MPA, but the catches in areas open to fishing are proportional to the areas open to fishing, resulting in catches proportional to the underlying vulnerable biomass. This scenario represents an equal distribution of effort over the underlying population distribution. In scenario 2 we allowed high catches in specific model cells on an ongoing basis, and therefore allowed the potential for corresponding high levels of crowding of fishing vessels on the water, and potentially high levels of localised depletion. In an actual fishery this would likely result in a dramatic reduction in catch rates over time in those cells and fishers would likely move to other cells with higher catch rates (Sanchirico 1999). Similarly, fishers are likely to explore new areas for potential high catch rates, following the Ricardian notions of resource exploitation (Sanchirico 1999). We distributed the catch in each cell proportional to the underlying vulnerable biomass of the fish population to implement spreading of the fleet in scenario 3.

Finally in Scenario 4 we investigate the impact of fishing the entire population proportional to the unfished vulnerable biomass (in 1995) throughout the Ross Sea region. In this scenario there are no closed areas. This scenario is not practically tenable but represents a distribution of catches which would not lead to spatial bias in the stock assessment.

2.3. Performance metrics

At the population scale, we investigated the potential effect of the proposed change in spatial management on the catches limits of toothfish, under the existing CCAMLR harvest management rules ($SSB_{50\%}$) for each of the spatial management scenarios investigated. The level of depletion of the spawning stock biomass is identical for all models as it is dictated by the management rules. We also calculated the expected overall catch rates in 2048 for the entire Ross Sea region.

At the zone scale (shelf, slope and north), we investigated likely changes in the regional population, which is important because toothfish in each zone occur at different stages of their life cycle. Metrics used in this investigation were levels of depletion of the total biomass in each zone at the end of the study period (in 2048) compared with the unfished population (in 1995); and the mean toothfish age in each zone in 1995 and in 2048, to represent changes in the demographic structure of the population.

At the scale of the spatial model cell, we examined levels of localised depletion in each cell at the end of the 35 year projection. Typically, one aim of MPAs is to reduce impacts in particular locations where extractive activities may constitute a particular threat to another part of the ecosystem such as foraging birds for example, but in the context of an existing fishery this can also be expected to increase impacts in other locations. To illustrate depletion, we order the initial biomass in each cell in decreasing order and chose the cells which cumulatively contain 80% of the total biomass. For this minimum area containing 80% of the unfished biomass, we report the proportion of cells at the end of the 35 year projection in which depletion is either above 75% of their unfished biomass (high depletion), or less than 25% of their unfished biomass (low

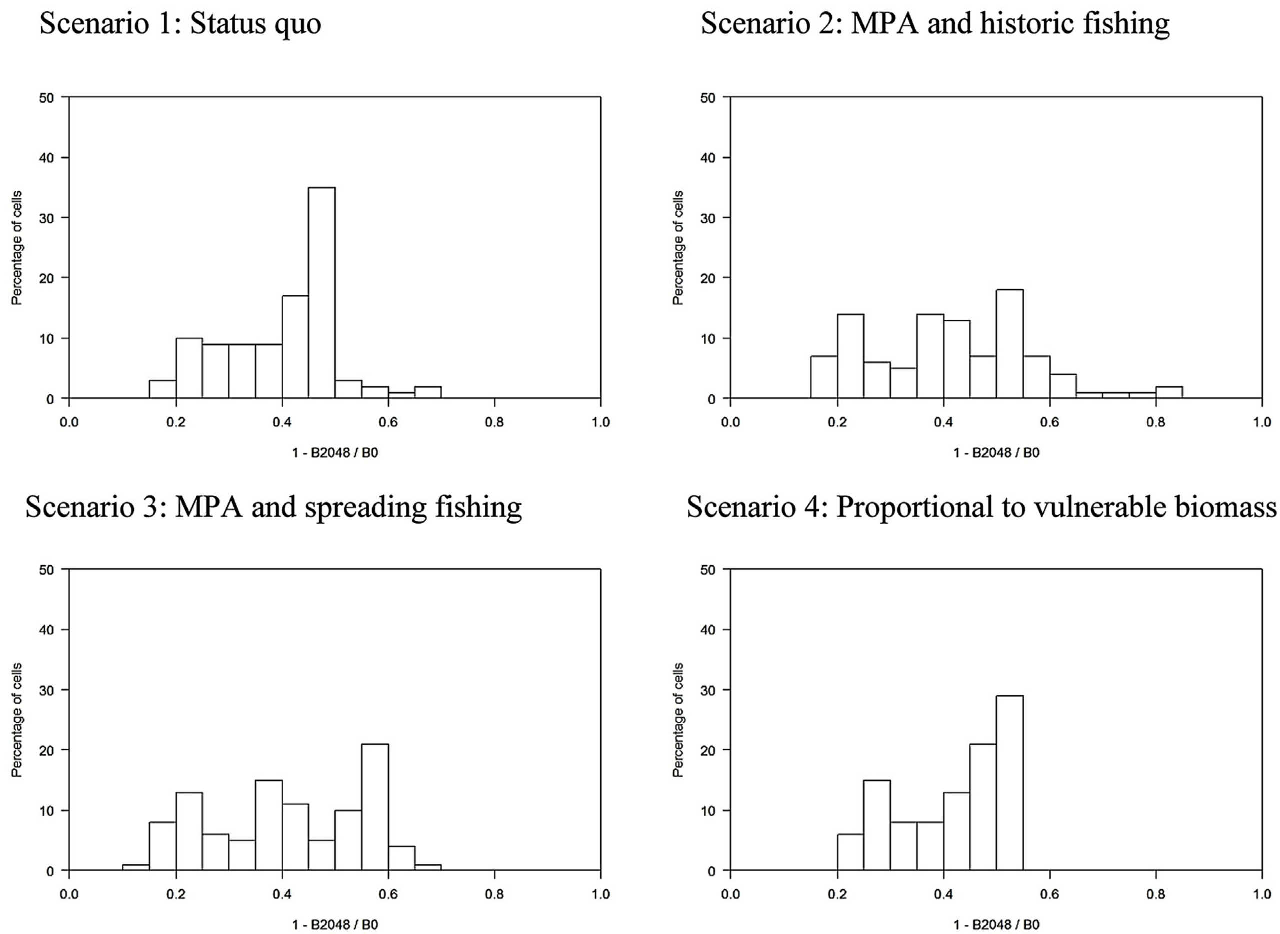

Fig. 6. Histogram of depletion levels as the proportion of the total unfished biomass per cell in 2048.

depletion). We also report the level of localised depletion in the most depleted cell under each scenario.

We calculated the Gini index and the minimum area containing 80% of the biomass in 2048 (Reuchlin-Hugenholtz et al., 2015) to describe the spatial distribution of total biomass at the end of the forecast period. The Gini index is a measure of statistical dispersion (i.e., in biomass across the domain), bounded between 0 when there is complete uniformity of the data, and 1 when there is maximal inequality. It is calculated as the area between the 1:1 line and the Lorenz curve which is the cumulative distribution of biomasses in the cells. It is calculated using the R package "ineq" (Zeileis, 2014). The minimum area containing 80% of the biomass (D80) is a measure of concentration of the population, and is calculated by ordering the biomass in each cell in decreasing order and reporting the number of cells which cumulatively contain 80% of the biomass. These indices were also calculated in 2013, at the start of the simulation years.

3. Results

Total unfished biomass for all models was 103,840 t, and the depletion level at the end of the projection period was 35% of total biomass (status of 75% of initial biomass), and 50% of spawning stock biomass. The MPA would displace fishing effort away from the shelf, reducing the share of total catch coming from the shelf zone from 40% to 15%. In the simulations, most of the displaced catch would be moved to the north, where the proportion would increase from 14% to 30% of total catch; the balance of displaced catch would move to the slope. At the level of the model cell, scenario 2 would result in a highly spatially concentrated fishing distribution, with very high catch levels in a single cell of the slope and relatively high catch levels in a few cells in the north (Fig. 4, top right panel). In contrast, scenario 3 would spread catch more evenly than scenario 2 across the slope zone, and also across the north zone (Fig. 4, bottom left); there would still be concentration of catches compared with scenario 1 (status quo). Scenario 4 would spread the catch across fishable habitats of the entire Ross Sea region, with about a third of the catch coming from each of the shelf, slope and north zones, proportional to the distribution of the vulnerable toothfish population in the Ross Sea region (Fig. 4, bottom right panel).

At the population scale, the ongoing status quo management of the fishery (scenario 1) provided the lowest long term catch limit of all four scenarios. Although the differences were modest (maximum difference of 6%), they represented between 1500 and 5500 t of additional catch over the 35 year projection for scenarios 2–4. Scenario 2, representing the RSR MPA with no spreading behaviour by the fishing fleet, achieved the highest catch limit, 6.0% higher than under current management. By implementing spreading behaviour by the fishing fleet under scenario 3, the catch limit increased by 4.2% relative to current management. Fishing proportional to unfished vulnerable abundance (scenario 4) provided an increase of 1.7% in catch limit compared to current management (Table 4). On the other hand, the expected overall catch rate in 2048 was highest for scenario 1, the status quo scenario. This catch rate was still 22% lower than that in 2013, as the toothfish biomass gets fished down. Displacing the fishing fleet away from some of its historical fishing grounds would result in a 16% to 22% reduction in the overall catch rate in 2048 compared with the status quo (Table 4).

At the zone scale, scenarios 2 and 3 (involving implementation of the MPA) resulted in the lowest level of depletion on the shelf (23% depletion compared with unfished biomass, instead of 28% and 26% depletion for scenarios 1 and 4, respectively), but slightly higher depletion levels in the north (51% depletion compared with 47% and 49% for scenarios 1 and 4, respectively). However the final biomass on the slope did not vary between scenarios and remained about 40% depletion Mean ages in each zone decreased between the inception of the fishery and 2048, but there was very little difference between the scenarios showing no dramatic change in the age structure of the population due to the change in the spatial distribution of fishing (which targets different age classes).

At the scale of the spatial model cell (Figs. 5 and 6, and Table 4), the status of the most depleted cell at the end of the 35 year projection period was depleted by 84% compared with its unfished total biomass under scenario 2 (MPA with no spreading behaviour by the fishing fleet); depleted by 64–68% under scenarios 1 and 3 (current management, or MPA with spreading behaviour by the fishing fleet); and depleted by 54% under scenario 4 (fishing proportional to unfished vulnerable biomass). The most depleted cell in 2013 was depleted by 39%. Under scenario 2, in which the MPA was implemented and fishing effort did not redistribute in space, the most highly depleted cell presented a lower total biomass than was observed under continued implementation of current management and a larger proportion of cells demonstrated high depletion levels compared to current management. In contrast where spreading fishing fleet behaviour enabled redistribution of catches in space (scenario 3), the localised depletion in the most depleted cell was comparable to that observed in scenario 1, and the distribution of depletions was more even throughout the Ross Sea region. Unsurprisingly, no cells were depleted beyond 50% of unfished biomass in scenario 4, as catches were directly proportional to the unfished biomass of the toothfish population (all cells were between 20 and 50% depletion).

Of the cells containing 80% of the unfished biomass (using the minimum area technique), the proportion of cells with low levels of depletion (defined as less than 25% depletion compared with their unfished total biomass) was about 12% in 2048 under the current management regime or when fishing proportional to the underlying biomass (scenarios 1 and 4), 20% in 2013, and 38–40% in 2048 in the two scenarios with implementation of the MPA (scenarios 2 and 3). High localised depletion (more than 75% depletion compared with unfished biomass) was observed only under scenario 2, in which 2% of cells containing 80% of the unfished biomass were depleted by more than 75% of their unfished biomass. The gini index and the D80 index in 2048 did not show substantial differences between the four scenarios, indicating there is no large differences in terms of distribution of the biomass or extent of the stock between the different scenarios. They showed an increase in dispersion compared with 2013, and a small reduction in the extent of the core area of the stock, consistent with the continued fishing down period to 2048.

4. Discussion

At the scale of the entire toothfish population, results indicate a likely small increase in the catch limit under the RSR MPA, or when fishing effort is distributed proportional to the underlying toothfish biomass. This modest change is likely due to the shift of the fishery away from the smaller juvenile fish on the shelf and toward larger mature fish on the slope and in the north. Similar effects have been documented elsewhere (e.g., Colloca et al., 2015; Edwards and Plagányi, 2011). We used the single area stock assessment model for Antarctic toothfish (Mormede et al., 2014a) to calculate the potential impact of a change in future catch split on the catch limit. Stockastic yield estimates which satisfy the CCAMLR harvest management rules were calculated using the MCMC estimations of the model parameters and different future catch selectivities (in effect different catch splits between the shelf, slope and north fisheries of the model). The expected increase in catch limit from a fishery targeting only juveniles in the south vs. one targeting only spawning adults in the north was +8%. Actual current fishing practices with 28% of the catches on the shelf where smaller fish reside, 46% on the slope where mostly adults reside and 14% in the north spawning grounds resulted in a catch limit midway between these two simulated extremes (Mormede et al., 2014a). These model results are consistent with the results obtained here through spatial modelling (Table 4), including the modest increase in catch limit in scenario 4 where 30% of the catch is in the north.

Studies on the effects of MPAs tend to show a negative effect of proposed marine protection areas on fishery revenue (e.g., Bastardie et al., 2014; Holland, 2000). In this study the catch limit will remain similar or increase slightly with the introduction of the MPA. This result might be explained by the CCAMLR management process which is catch-limited rather than effort-limited, the move to fishing more mature fish, and/or that the fishery is still in fishing-down phase. It is likely this potential increase in annual revenue will be moderated by a reduction in the catch rate of the fishery due to its displacement to less productive fishing grounds. The drop in catch rates was estimated at between 14% and 22% as the scenarios move catches away from the highest catch rates. The overall benefit or cost of the RSR MPA to the fishing industry will depend on the running costs of each individual vessel and their current and future fishing patterns.

At the scale of zones within the Ross Sea region, the MPA is expected to affect the relative distribution of toothfish biomass between the Ross Sea shelf vs. the slope and northern zones, with potentially important implications for the ecosystem. The Ross Sea shelf is one of the most ecologically productive locations in the entire Southern Ocean (Arrigo et al., 1998), with abundant pelagic prey supporting large and diverse top predator populations during the annual summer sea ice retreat (Ainley, 1985). The RSR MPA is intended to prevent trophic competition with important pelagic prey species in this key area (e.g., Hooker and Gerber, 2004). The Ross Sea shelf is also a preferred and likely a critical feeding ground for top predators that may be seasonally reliant on toothfish for prey (Ainley and Siniff, 2009; Pitman and Ensor, 2003); maintaining a high biomass of toothfish in this zone would reduce the risk of localised trophic competition between predators and the fishery in preferred foraging areas. The MPA will also protect diverse benthic communities on the shelf (Clarke and Johnston, 2003; Parker and Bowden, 2010), although bottom fishing impacts from longlines in the Ross Sea region are estimated to be very low (SC-CCAMLR-XXXII, 2013; Sharp et al., 2009).

In contrast to expected outcomes on the shelf, under the RSR MPA, toothfish biomass in the north is likely to be reduced to a lower level than would occur under status quo management. It is expected this effect is mainly due to the increase in catches displaced from the shelf and slope areas to the north area. Localised depletion in spawning areas might be expected to affect toothfish recruitment if spawning biomass were reduced to very low levels but this is unlikely under current CCAMLR harvest management rules (Hanchet et al., 2015b).

At the scale of the spatial model cell (cell size 24 000 km^2), implementation of the RSR MPA resulted in a large increase in the number of cells where toothfish abundance was only lightly depleted (by less than 25% of unfished biomass). Moreover, assuming spreading behaviour from the fishing fleet to optimise their catch rates, implementation of the MPA produced only very minor changes in the level of localised depletion observed in the most depleted cells, and in the number of cells highly depleted (by more than 75% of their original biomass). This result indicates that under the RSR MPA scenario and simulated catch splits among zones, redistribution of catch to other locations open to fishing may effectively alleviate the increased risk of localised depletion in preferred fishing locations. Under the scenario in which fishing effort distributions remained on the most productive grounds (scenario 2), higher levels of localised depletion occurred, but this scenario is probably unrealistic as the fleet is likely to respond in some way to optimise long-term catch rates unless constrained by other factors (e.g. other management measures or unfavourable ice conditions), and crowding issues would ensue if the effort was strongly concentrated. Conversely, fishing in proportion to the spatial pattern of unfished vulnerable biomass (scenario 4) provided the most uniform level of depletion, but this scenario is unlikely to be achievable in practice, requiring very low catch levels spread over a large area; furthermore fishing in some of these locations may compromise objectives of the MPA. Although some of these metrics are somewhat arbitrary, they are indicative of likely effects when shifting extractive processes away from specific locations. The coarser gini index at the level of the stock showed no likely difference in the general distribution of biomass between the different scenarios, and likewise the D80 index showed no difference in the extent of the stock between these scenarios. Both these indices tracked the fishing down period from 2013 to 2048, with an increase in the gini index and a decrease in the D80 index through that period.

While the likely effects of the RSR Marine Protected Area is the focus here, the same approach is applicable where alternate spatial management scenarios are considered. Evaluation of the potential effects of alternate spatial management scenarios, in particular the likely consequences for biological distributions and related patterns of human resource use, will likely become both more necessary and more challenging as plans to implement 'marine spatial planning' proceed in areas subject to multiple and conflicting management demands (Crowder and Norse, 2008; Pikitch et al., 2004; Young et al., 2007). Spatially explicit models offer a valuable tool to inform such evaluations (e.g., Lehuta et al., 2013), with simulations showing the design of MPAs is likely to impact both their effectiveness and their effects on fisheries, and therefore need to be designed consistent with spatial modelling advice. We have showed that implementing the RSR MPA can be expected to result in a slightly higher catch limit for the fishery but lower catch rates. At a fine scale, it might also result in an increase in the portion of available toothfish habitat experiencing only minimal localised depletion, and little change in the proportion of the available habitat experiencing substantial localised depletion. This MPA would also result in more toothfish biomass available in preferred top predator foraging locations of the Ross Sea shelf, consistent with one of the stated objectives of the MPA. These results are conditional on the catch distributions as described in Table 3 but that a 19% and not 30% of the catch limit has been temporarily allocated to the north for the RSR MPA and therefore concentration of catches and associated levels of depletion on the slope are likely to be higher than forecast, at least in the short term while further data are collected. Furthermore, catch distributions will also vary depending on ice conditions, fleet composition, and markets to name but a few. Finally, should the life cycle of toothfish and therefore its movement and biomass distribution deviate drastically from that described in the model, then results could differ from those predicted. The model was selected based on best fit to the data, and that sensitivities carried out with varying potential life cycles showed that the life cycle described not only fits our biological understanding but also provides the best model fit to the data available.

The results are consistent with that from other modelling studies of the potential effects of MPAs on fish populations. Dueri and Maury (2013) showed that the effects of proposed MPAs depended not only on the location of the MPAs but also on the evolution of the fisheries and that different fishery scenarios needed to be investigated. Abecasis et al. (2014) highlighted that the effectiveness of MPAs depended on the home range of fish, and movement was inextricably linked to the potential for protection. Fouzai et al. (2012) used a calibrated Ecopath with Ecosim model of the northern-central Adriatic and predicted potential MPA scenarios using ecospace. In their study, the whole of ecosystem was included in the modelling and the effects of the MPA on various parts of the ecosystem were quantified simultaneously. Such a method would allow the investigation of the effectiveness of the proposed MPA not only on the commercial fish species but also the entire ecosystem, although would probably be unlikely to be used for tactical decisions on fish stocks specifically (e.g., Fulton et al., 2003).

We have shown that spatially explicit population models can inform the design of marine protected areas such as that proposed for the Ross Sea region, in this instance investigating the effect on the toothfish resource. To realise their full potential, models should be fully evaluated against available data, and iteratively improved as new data become available. The model used in this simulation study showed adequate fits to existing fishery data and was in general agreement with the spatial characteristics of the population, but did not capture fine-scale patterns (Mormede et al., 2014b). This model has not yet been tested with fishery independent data; research is currently underway to collect such data. While the application to the Ross Sea fishery and the investigation of the likely effects of a proposed Marine Protected Area on toothfish were the focus here, this approach is applicable anywhere that alternate spatial management scenarios that may displace fishing effort are considered. Using end to end ecosystem models would also allow the investigation of alternative spatial management scenarios on all parts of the ecosystem simultaneously.

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