

**To be completed by the Secretariat:**

Document No.: WG-EMM-14/51  
Date submitted: 23 June 2014  
Original Language: English

**To be completed by the author:**

Meeting: WG-EMM-2014  
Agenda Item No(s): 2.1.5

Title **Development of a spatially-explicit minimum realistic model for Antarctic toothfish (*Dissostichus mawsoni*) and its main prey (Macrouridae and Channichthyidae) in the Ross Sea**

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Published or accepted for publication elsewhere? Yes  No

If published or in press, give details:

To be considered for publication in *CCAMLR Science*?<sup>1</sup> Yes  No

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**Abstract**

To explore the potential effects of the toothfish fishery on the population dynamics of Antarctic toothfish and its main prey, grenadiers (Macrouridae) and icefish (Channichthyidae), we develop a spatially explicit model using a predator-prey suitability model for the Ross Sea Region. We model the age-based population dynamics of toothfish, grenadier, and icefish, and include natural mortality ( $M1$ ) and predation mortality ( $M2$ ), in addition to fishing mortality ( $F$ ) on all three species. The model suggests that the predation release caused by the fishery effect on toothfish abundance is greater than the direct fishing mortality on both prey species and that icefish is expected to show a larger increase in biomass through time than grenadiers. It also suggests that a prey-suitability function is more likely than a Holling type II function to describe the predatory relationships in the model. We use the model to compare the predicted population changes with available abundance data for each species to develop hypotheses of the nature of the interaction. Whilst this model is in a development stage, it provides a useful tool for evaluating potential impacts of the fishery on key prey species, and for assessing and designing monitoring tools for fish species associated with the toothfish fishery. We recommend targeted sampling of toothfish for diet analysis, and the monitoring of icefish and grenadier populations in SSRUs 88.1H and 88.1K through the development of age frequencies (length measurements and aging).

Keywords: Ross Sea, predator, prey, spatial population model, ecosystem model, Antarctic toothfish

# **Development of a spatially-explicit dynamics model of Antarctic toothfish (*Dissostichus mawsoni*) and its main prey (Macrouridae and Channichthyidae) in the Ross Sea**

## **Introduction**

Toothfish are the major finfish currently exploited in the Southern Ocean, with only krill exceeding the catch in recent years (Secretariat 2013). In the Ross Sea sector of Antarctica, over 99% of the catch is Antarctic toothfish (*Dissostichus mawsoni*, henceforth “toothfish”)(Secretariat 2013).

The toothfish fishery in the Ross Sea region has been operating since 1997, managed under the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR, see SC-CAMLR-XXXII 2013). CCAMLR Article II paragraph 3(b) requires that fishing shall be conducted in a way that maintains the “ecological relationships between harvested, dependent and related populations”. Current CCAMLR management of predatory finfish is predicated on the assumption that this principle will be satisfied in a precautionary manner (i.e. irrespective of variations between systems) if a given toothfish stock is reduced to 50% of unfished spawning biomass.

Knowledge of the trophic relationships among species is a vital step in identifying potential indirect effects of fishing. Changes to prey communities resulting from changes in predator populations are predicted to be strongest where the predator is large, mobile, and has high metabolic rate, where prey species are long-lived, functional predator diversity is low, or predator intra-guild predation is weak or absent (Heithaus et al. 2008, Shurin et al. 2002). Many of these factors are present in the Ross Sea ecosystem (Pinkerton & Bradford-Grieve 2014). On the Ross Sea continental slope, where the majority of the Antarctic toothfish population is likely to feed (Hanchet et al. 2008), toothfish are likely to be the major predators of grenadier (*Macrourus whitsoni* and *M. caml*) and icefish (*Chinobathyscus dewitti*) (Bury et al. 2008, Pinkerton et al. 2010). Both species of grenadier and icefish are also the main species taken as bycatch in the longline fishery in the Ross Sea (Hanchet et al. 2014).

There are various ways to model trophic ecosystem dynamics. There are individual-based models such as OSMOSE (Shin & Cury 2004) and whole ecosystem or “end-to-end models” such as Ecopath with Ecosim (EwE, Christensen & Walters 2004) and Atlantis (Fulton 2010) which include a representation of the entire ecosystem to various levels of detail, from plankton to top predators and in some cases environmental influences and land uses. A carbon balanced trophic model of the Ross Sea shelf and slope using (EwE, Christensen & Walters 2004) was developed by Pinkerton et al. (2010). Based on the model, it is likely that trophic effects caused by a reduction in the spawning stock biomass of toothfish will be greatest for medium sized (40–100 cm) demersal fish (predominantly grenadiers and icefish) in this region(Pinkerton & Bradford-Grieve 2014). However, whilst such models are useful for broader strategic decision making and examining hypothetical scenarios, they lack the spatial, temporal resolution to provide more tactical management advice. Minimum realistic models (MRMs) have been developed that focus on a small number of species or groups of species and a restricted type of interaction (e.g., Punt & Butterworth (1995), Mori & Butterworth (2004), and (Begley 2005)).

We aim here to develop a minimum realistic representation of the system dynamics. By “minimum realistic” we mean that the model needs to be able to capture the key factors and processes that determine the dynamics of the components of interest. Minimum realistic models (MRMs) restrict themselves to a small number of species or groups of species and a restricted type of interaction. As such MRMs are distinct from individual-based models such as OSMOSE (Shin & Cury 2004) which follow each individual fish, and whole ecosystem or “end-to-end models” such as Ecopath with Ecosim (EwE, Christensen & Walters 2004) and

Atlantis (Fulton 2010) which include a representation of the entire ecosystem, from plankton to top predators and in some case environmental influences and land uses. Examples of MRMs include those developed by Punt & Butterworth (1995), by Mori & Butterworth (2004), and GADGET (Begley 2005)

Key dynamics that the Ross Sea Region MRM must be able to represent in order to simulate plausible scenarios include:

- Change in biomass of Antarctic toothfish over time. This should be resolved spatially (at least to some extent), and by size/age of toothfish (as this affects predation on different prey groups);
- Removals of prey groups due to bycatch in the fishery under various management scenarios;
- Intrinsic production rate of prey groups involving an estimate of biomass, recruitment rate, and fish growth rate;
- Consumption rate of demersal fish species/groups by Antarctic toothfish;
- Diet of Antarctic toothfish, including how this may change as the relative abundances of prey changes over time;
- Availability of demersal fish prey groups to Antarctic toothfish, including assessing spatial overlap between species within the study region; and
- The potential influence of other prey items of Antarctic toothfish (e.g. squid) on model results.

The purpose of this study is to develop a minimum realistic model of the interactions between toothfish and these two main groups of demersal fish prey in the Ross Sea region (Figure 1). The model developed is spatially-explicit because there is spatial heterogeneity within the Ross Sea region in the distribution of toothfish, the distribution of each prey species, the distribution of fishing effort, and in the observed diet of toothfish. We assess its performance in representing changes observed in the fishery data. We also use the model to assess and design monitoring plan objectives for fish species associated with the fishery.

## **Methods**

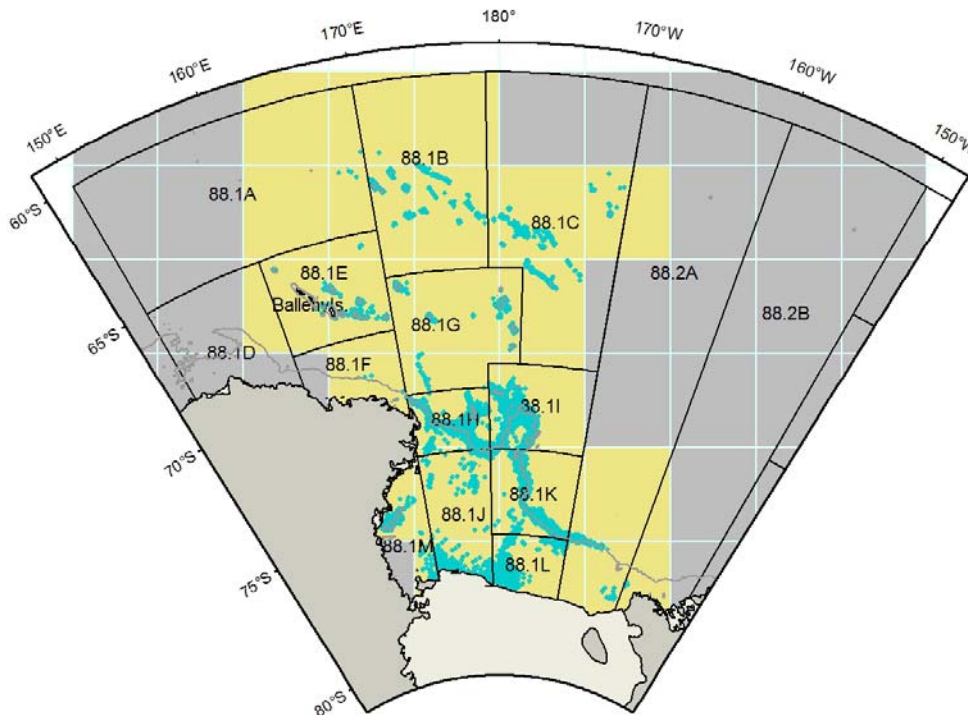
### ***Modelling framework***

The MRM developed is a generalised Bayesian model which allows both fitting to data and simulation, though here the model was implemented as a simulation model, i.e. with no fitting to data. Populations of toothfish, grenadiers and icefish in the MRM were age-based (but not differentiated by sex) with each species/group having a maturity ogive (see below) and Beverton-Holt stock recruitment relationship with steepness of 0.75 (Punt et al. 2005).

The model was spatially-explicit and was developed using the Spatial Population Model (SPM) software (Dunn et al. 2012). The spatial structure of the model was represented by dividing the Ross Sea region into 60 equal area (118,300 km<sup>2</sup>) cells, with the fish populations restricted to the 22 cells where the depth was suitable for toothfish habitat and fishing has previously been carried out (Figure 1). The underlying distribution, abundance, and movement patterns of Antarctic toothfish has previously been derived using the SPM framework (Mormede et al. 2014b). The spatial distributions of grenadier and icefish were defined by the distribution of catch per unit effort (CPUE) in space; whilst their total abundance was derived from toothfish consumption rates. Movement between cells for the prey species was assumed to be negligible but this movement hypothesis was tested in the model framework.

Two predator-prey relationships were investigated: the Holling type II function and a prey suitability predation function (both described below). Only the prey suitability predation option was implemented spatially as this gave more plausible results.

We assumed that mortality of grenadier and icefish was solely due to toothfish predation. Whilst Rassweiler & Rassweiler (2011) suggested that predation is the principal cause of adult fish mortality, others have suggested a residual non-predation mortality of up to 20% (e.g., Alaska Fisheries Science Center 2012). Assuming no residual non-predation mortality will provide the most extreme of responses of the prey species to a change in toothfish biomass.



**Figure 1: The Ross Sea region and CCAMLR SSRUs. Each equal area cell represents a cell in the spatial model, then restricted to the 22 cells colours yellow where fishing has been previously carried out. The blue dots represent fishing effort, and the grey line the 1000m depth contour.**

### *Toothfish diet*

The diet of Antarctic toothfish has been studied based on stomach content samples collected from the fishery (e.g., Stevens et al. 2012). In particular, the eastern part of SSRU 88.1H (Figure 1) has been the subject of extensive sampling to investigate potential changes in the diet of toothfish as an ecosystem indicator (Stevens et al. 2012). Although diet through time was characterised from this targeted sampling, there was no statistically significant change (Stevens et al. 2012). Grenadier and icefish each represented 25% by weight of toothfish diet in that area in 2003. The next most important prey group (Muraenolepididae) represented 14% of the diet, with cephalopods representing 12%, notothenioids 5%, and other species groups less than 5% each. Some of these species could be incorporated in future models, but are not taken as bycatch of the fishery. At this stage the model was confined to the top two prey species groups, representing ~50% by weight of toothfish diet, and also species caught as bycatch in the fishery.

Toothfish are likely to account for most of the natural mortality of grenadier and icefish (Pinkerton et al. 2010). Other potential top predators of grenadiers and icefish were ignored as insignificant sources of additional mortality (Pinkerton et al. 2010).

The consumption rates of fish reported in the literature vary largely depending on a number of factors such as fish species, water temperature and prey species. For example, Palomares & Pauly (1998) suggested a value of 1.8 year<sup>-1</sup> but the multi-species program OSMOSE uses a value of 3.5 year<sup>-1</sup> based on the work of Longhurst & Pauly (1987) on fish on coral reefs. Therefore an alternative choice of this parameter could halve or double the impact of changes in toothfish population on the prey species. An initial estimate specific to Antarctic toothfish in the Ross Sea region based on growth was calculated at 1.4 y<sup>-1</sup> (Pinkerton, pers. comm.). Therefore the published value of 1.8 year<sup>-1</sup> was used until a published value specific to Antarctic toothfish is available.

### ***Grenadier and icefish biomass***

We assume that before the start of the fishery, all three species were in equilibrium whereby the biomass of each was stable in time. In order to achieve this, predation mortality due to toothfish was assumed to be equal to the natural mortality for both grenadier and icefish. For example, for grenadier, the predation mortality ( $U_M$ ) by toothfish would equal the biomass of grenadier lost to natural mortality ( $B_M$ ) as described by equation 1.

$$U_M = B_M \cdot e^{-M_M} \quad (1)$$

### ***Predator-prey functions***

The Holling type II function (Holling 1959) removes the biomass of grenadier and icefish ( $U_M$  or  $U_I$  respectively) according to their local biomass ( $B_M$  and  $B_I$  respectively) and the local biomass of toothfish ( $B_T$ ), but constrained by a maximum exploitation rate ( $a$ ). The slope of the relationship is controlled by a parameter ( $b$ ) which allows a range of responses from a hungry predator to a satiated predator. For example, in the case of grenadier, the removals are as follows.

$$U_M = B_T \frac{(a \cdot B_M)}{(b + B_M)} \quad (2)$$

Two scenarios were carried out: parameter  $b$  was defined as either equal to the prey biomass for a satiated predator, or equal to a tenth of the prey biomass for a hungry predator. Parameter  $a$  was then calculated so that the mortality due to predation before the start of the fishery was equal to natural mortality, using equation 1.

The predator-prey suitability function was based on MSVPA functions described by Jurado-Molina et al (2005). The aim was to allow a greater ability of the predator to modify its diet when one species became more dominant. As icefish is far more productive than grenadier, this constraint did arise when using the Holling functions. With a predator-prey suitability function, the local mortality of grenadier and icefish ( $U_M$  or  $U_I$  respectively) is a function of the toothfish diet fraction of each prey ( $DF_M$  and  $DF_I$  for grenadier and icefish respectively), its assumed consumption rate from the literature ( $CR=1.8$ , and the local biomass of toothfish ( $B_T$ ) as determined by the spatial model of that species (Mormede et al. 2014a). For example, for grenadier, the removals are described by equation 3 below.

$$U_M = B_T \times CR \times DF_M \quad (3)$$

The diet fraction of each prey is a function of the electivity of the predator for its prey ( $E_M$  and  $E_I$  respectively) and the availability of the prey species ( $A_M$  and  $A_I$  respectively) relative to the availability of the other prey species. Diet fraction for grenadier is expressed in equation 4, and electivity in equation 5. Electivities are nominally defined as summing to 1.

$$DF_M = \frac{E_M \cdot A_M}{\sum_{\text{all prey}} (E_{\text{prey}} \cdot A_{\text{prey}})} \quad (4)$$

$$A_M = \frac{B_M}{\sum_{\text{all prey}} [B_{\text{prey}}]} \quad (5)$$

The values of electivity for grenadier and icefish were calculated assuming equilibrium prior to fishing as per equation 1, and assuming the diet fractions of 0.25 for each species, as described by toothfish diet data. Electivities of grenadier and icefish were calculated as 0.17 and 0.83 respectively, reflecting the lower productivity and hence higher biomass of grenadier compared with icefish to achieve the same diet fraction at equilibrium.

### ***Species biology***

Toothfish biology and life cycle in the Ross Sea region has been extensively described (e.g., Hanchet et al. 2008, Hanchet et al. 2010, Horn et al. 2003, Parker & Grimes 2010). The biological characteristics of species caught as bycatch in the toothfish fishery in the Ross Sea region have also been described (e.g., Francis & Gallagher 2009, Pinkerton et al. 2013, Stevenson et al. 2012, Sutton et al. 2008), with abundance of grenadiers and icefish on the slope of the Ross Sea Region estimated by Hanchet et al (2009). Estimates for life history parameters for toothfish are summarised in Table 1.

The life history characteristics of *Macrourus whitsoni* are used to represent all grenadier in the model although recent studies have shown grenadier in the Ross Sea region are comprised of at least 2 species which have different life history characteristics (Pinkerton et al. 2013). The life history characteristics of *Chionobathyscus dewitti* are used to represent all icefish as this species is expected to represent the majority of icefish present on the slope of the Ross Sea region (Sutton et al. 2008). Grenadier and icefish have very different life histories. Whitson's rattail (*Macrourus whitsoni*) has a natural mortality rate of  $0.084 \text{ y}^{-1}$  (i.e., a maximum age of about 55 years) (Pinkerton et al. 2013), whilst icefish (*Chionobathyscus dewitti*) has a natural mortality rate of  $0.485 \text{ y}^{-1}$  (i.e., maximum age of about 10 years) (Sutton et al. 2008). Estimates for life history parameters for each species are summarised in Table 1. Fishery selectivity at age was derived from reported length frequency and von Bertalanffy age length relationships as detailed in Table 1.

Grenadier and icefish are both taken as fishery bycatch, with grenadiers the largest bycatch of the fishery at about 180 t per year compared with 5 t per year for icefish) (Stevenson et al. 2012).

**Table 1: Biological parameters assumed for the modelling.**

Relationship	Parameter	toothfish	grenadier	icefish
Natural mortality	$M$ ( $y^{-1}$ )	0.130	0.084	0.485
Von Bertalanffy age-length relationship	$t_0$ (y)	-0.117	0.000	-5.590
	$k$ ( $y^{-1}$ )	0.091	0.060	0.100
	$L_\infty$ (cm)	174.5	84.1	57.67
Length-weight relationship	$a$	1.05e-8	1.75e-9	1.01e-9
	$b$	3.036	3.232	3.720
Maturity	$A_{50}$ ( $\pm A_{1095}$ )	12.2 ( $\pm 2.8$ )	12.0 ( $\pm 10.0$ )	3.5 ( $\pm 2.6$ )
Fishing selectivity	$A_{50}$ ( $\pm A_{1095}$ )	6.9 ( $\pm 2.7$ )	26.0 ( $\pm 8.0$ )	2.6 ( $\pm 1.3$ )

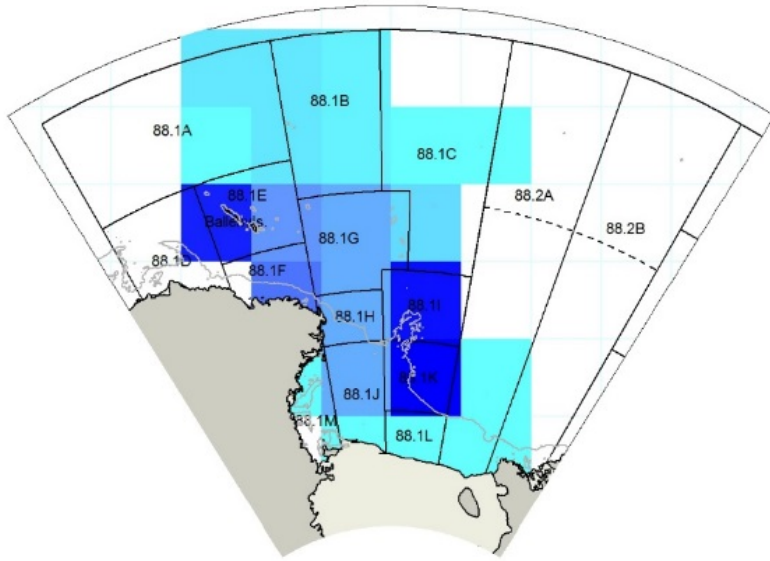
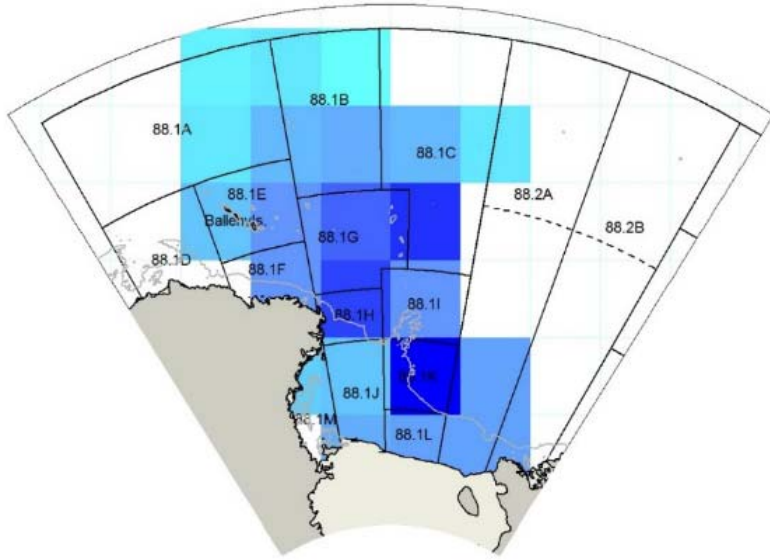
### *Species distribution and biomass*

The distribution of toothfish is characterised by ontogenetic movement to deeper habitats as they grow older, with spawning migrations to northern hills and seamount regions (Hanchet et al. 2008). The spatial distribution of toothfish was based on the spatial age-based population model developed by Mormede et al. (2014b) using the SPM framework (Dunn et al. 2012). This model allowed for the movement of toothfish during different various reproductive stages (e.g., immature, mature and spawning) based on depth, temperature, the presence of hill features based on depth data, and distance travelled, and was optimised using fishery observations catch rate, age and tag recoveries. The total biomass at the start of the fishery was derived from the single-area stock assessment of toothfish currently used for management purposes (Mormede et al. 2014a). As a result, the number of toothfish and their age distribution and biomass was estimated for each spatial cell in each year within the model.

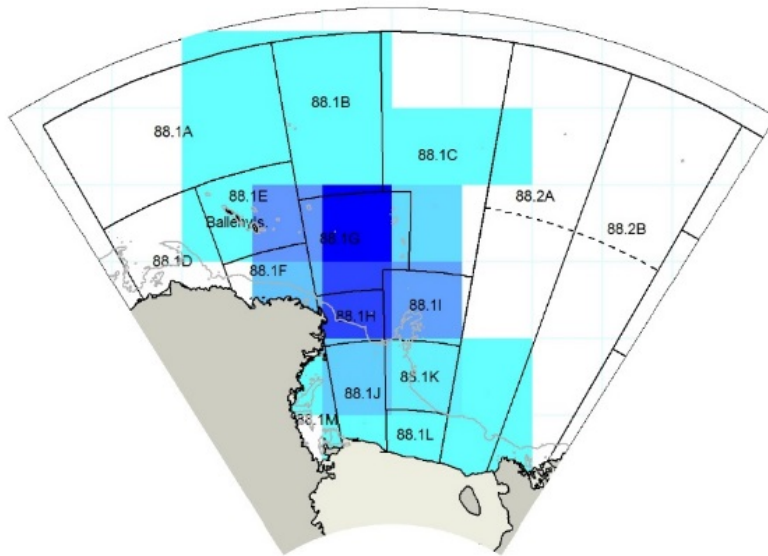
Two options for prey movement were investigated: either grenadiers and icefish did not move between cells (consistent with an observed lack ontogenetic movement, for example there was no evidence of changes in mean length of fish with depth or area), or they redistributed themselves proportionally to their original distribution as their biomass increased.

The biomass of grenadier and icefish in the model cell equivalent to SSRU 88.1H was calculated based on the diet fraction of each species in this area, toothfish consumption rate (see toothfish diet section) and the biomass of toothfish in this model cell, by applying equations 1 and 3 for each species independently. The biomass of both species in space was then obtained through scaling the toothfish fishery catch per unit effort (CPUE) for each species by the biomass obtained in the model cell equivalent to SSRU 88.1H. The CPUE for each prey species was standardised for effort (number of hooks) and gear type (only data from vessels using autoline systems was used).

We assumed that before the start of the fishery all three species were in equilibrium. An initial model was run with natural mortality for both grenadier and icefish and no predation. The consumption rates of toothfish in each cell which removed all of the icefish required was then calculated (equation 1). The distributions of grenadier and icefish only partly overlap, and do not cover the entire toothfish distribution range (Clark et al. 2010) (Stevenson et al. 2012), hence an extra mortality term per cell was added in order to remove the additional grenadier mortality required (in cells where no icefish were present). In the final run, the natural mortality term was replaced by the predation parameters. Both grenadier and icefish present in each spatial cell at the start of the fishery were assumed consist of their full age-frequency distribution since there was very weak evidence of any changes in their length distribution with space in the fishery data. The biomass distributions of toothfish, grenadiers and icefish are presented in Figure 2.







**Figure 2: Biomass distribution in space of toothfish (top), grenadier (middle) and icefish (bottom) in 1995. The CCAMLR Small Scale Research Units (SSRUs) are showed in black and the 1000m depth contour line in grey.**

## **Results**

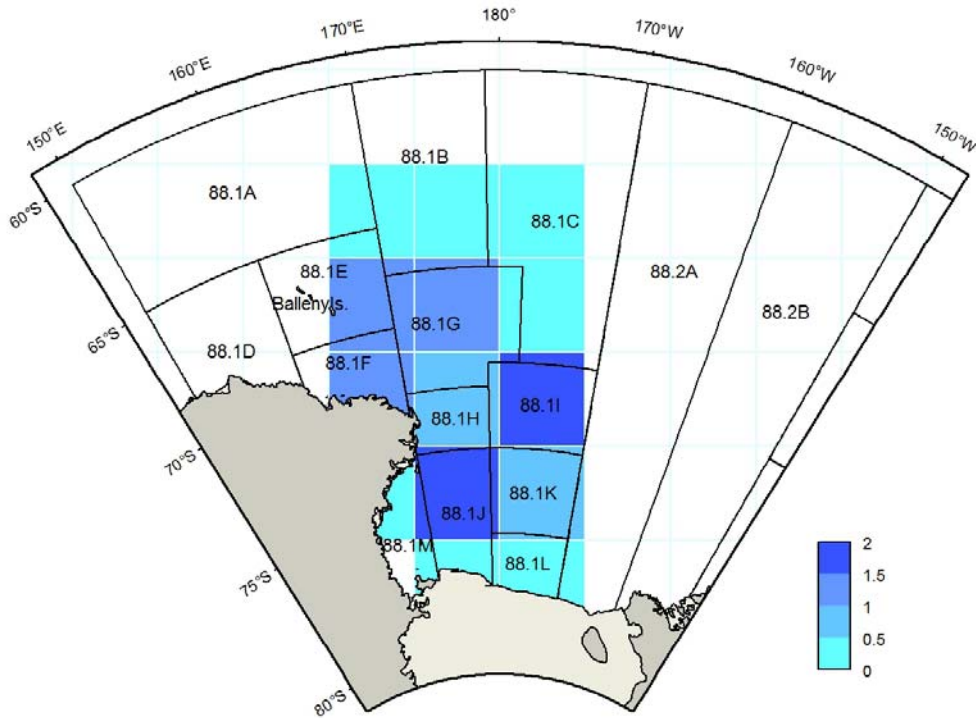
### ***Predator-prey relationships***

The Holling type II relationship resulted in a four to nine-fold increase in icefish total biomass, whilst grenadier biomass increased very little. Using prey suitability equations allowing a change in the diet composition of toothfish as prey proportions changed resulted in an icefish biomass of 230% of pre-fishery biomass and grenadier biomass of 115% of pre-fishery levels

### ***Balancing the spatial model***

The consumption rate in the various cells of the model varied between 0.12 and 1.85 year<sup>-1</sup> (Figure 3).

Once the consumption rates were calculated, the only cells requiring additional grenadier mortality were those where icefish were present in very small quantities, and therefore the consumption rate of toothfish was near zero for both species, requiring additional natural mortality for grenadiers.



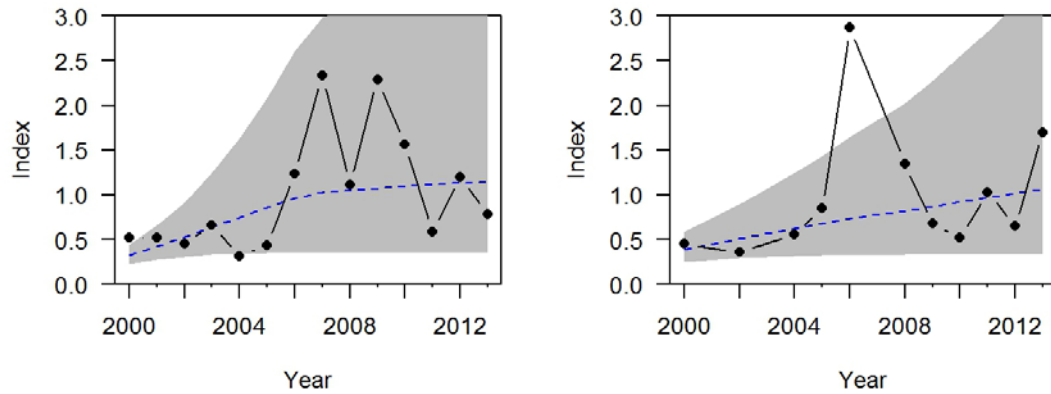
**Figure 3: Consumption rate in space, with CCAMLR SSRUs overlaid in black.**

The estimated biomass for each prey species on the slope area of the Ross Sea were compared with the estimates from the trawl survey (Hanchet et al. 2009). The biomasses calculated based on toothfish consumption rate were consistent with a catchability of 0.07 for icefish and 0.14 for grenadier. Although these are localised estimates of biomass for these two species based on a research survey, these assumed trawl catchability of 1 and therefore represent an estimate of biomass likely biased low.

### ***Movement of prey***

There was no strong indication of ontogenetic movement of icefish or grenadiers between cells, as length frequencies are similar in different areas. In contrast, larger toothfish were found in cells presenting deeper depths, and in the north where they are assumed to spawn.

The two movement options for prey species (redistribution or no movement) were tested by comparing the predicted change in icefish total biomass in SSRUs 88.1K and 88.1H (where the largest predicted changes occurred) with the documented changes in catch per unit effort (CPUE) from the fishery, standardised for gear type, number of hooks, and nation (Figure 4). Although the CPUE indices of icefish were variable, they presented a general increase in the biomass which was consistent with limited movement of icefish between cells in the spatial model (Table 2), at least in the timescale considered. The consistency in patterns between the two areas but also in the estimated change in icefish biomass would suggest that the model key parameters are similar those assumed here. As icefish is not a target species, CPUE is potentially a relatively useful metric of biomass change.



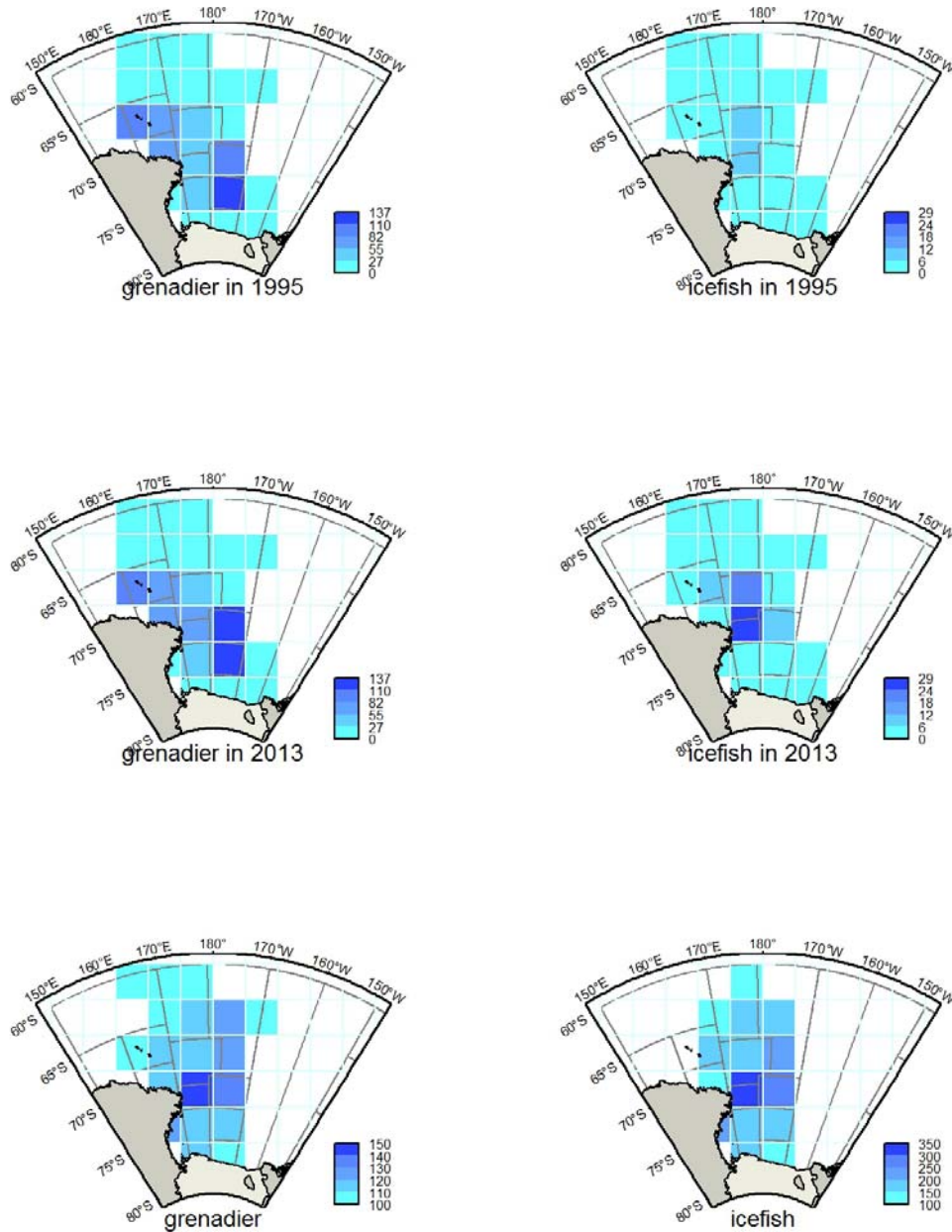
**Figure 4: Standardised CPUE for icefish in 88.1H (left) and 88.1K (right), with LOWESS smoothed rate of change in blue and associated 80% confidence interval in grey.**

**Table 2: Changes in the icefish total biomass in SSRUs 88.1H and 88.1K between 2000 and 2013 as estimated by standardised CPUE or the models assuming either no movement or movement of prey species between model cells. Values in parenthesis are the 80% confidence intervals of the increase.**

<b>B<sub>2013</sub> (%B<sub>2000</sub>)</b>	<b>In SSRU 88.1H</b>	<b>In SSRU 88.1K</b>
Based on CPUE	350% (150 – 825)	280% (130 – 590)
Model with no prey movement between cells	340%	215%
Model with prey movement between cells	200%	200%

### *Population changes*

Aggregated at the level of the Ross Sea region, the total biomass of toothfish in the model was reduced to 77% of the initial biomass since the start of the fishery which resulted in an increase in grenadier total biomass to 115% of initial biomass, and icefish to 215% of initial biomass in the models. By cell, the increase in grenadier biomass ranged from 100% to 150% of initial biomass, and icefish from 100% to 350%. The largest changes were predicted in SSRU 88.1H, where almost 30% of the toothfish catches have occurred. The relative spatial distributions of grenadier and icefish in 1995 and 2013 are shown in Figure 5.



**Figure 5: Biomass of grenadier and icefish in 1995 (prior to fishing) and 2013, and percentage biomass change between 1995 and 2013 (bottom figures).**

### Model validation and discussion

The models developed here describe potential trophic interactions between toothfish and its main prey in the Ross Sea region. The predation function was assumed as either a Holling type II or a prey-suitability function with an assumed consumption rate of toothfish. The biomass changes using a prey-suitability function were more likely than that obtained using Holling functions as they predicted population changes which were more in agreement with the observed data. Models where prey species did not move between cells were also more consistent with CPUE data than models which assumed prey species redistributed to their preferred habitats each year. In SSRU 88.1H where most of the biomass change is expected in

the model, toothfish diet in the model shifted from a 50/50 proportion of grenadier to icefish, to a 30/70 proportion of grenadier to icefish, showing a clear shift towards icefish as the population of icefish increased faster than that of grenadier consistent with a more productive life history.

A single electivity per prey species for the entire model and a consumption rate per cell for toothfish accounted for the exact required removals of each prey species for the two prey species populations to be stable in each cell of the model despite the differing distribution of the two species in space. The lowest consumption rates were found in the northern hills. This is in agreement with isotope work which concluded that toothfish were likely to eat little while in the northern hills, where they migrate to spawn (Pinkerton et al. 2014a). The calculated consumption rates were also significantly negatively correlated with the proportion of empty stomach in each of the cells, based on fishery data collected in 2012-13. The upper consumption rate value of  $1.85 \text{ year}^{-1}$  in SSRU 88.1I seems high, particularly since grenadier and icefish only represent 50% of toothfish diet in adjacent SSRU 88.1H. However it would be consistent with either a higher proportion of the toothfish diet in this SSRU, or with a higher consumption rate as used in OSMOSE.

Biomass changes predicted by the model were compared with various observed data. The CPUE pattern for icefish was consistent with the biomass changes expected by the model. Stomach content data collected by the fishery over time were highly variable, and although a change with time was recorded, that change was not statistically significant because of low sample size (Stevens et al. 2012). The changes in length frequencies of the prey species were inconclusive due to the low sample sizes for these species. To resolve a spatial pattern in size of prey species with time, more intensive sampling of prey species length frequencies and predator diet are needed (potentially at a number of years' interval).

The population dynamics modelled here are conditional on the assumptions made. For example, if we assumed only 80% of mortality of each group was due to toothfish (e.g., Alaska Fisheries Science Center 2012), the biomasses of the prey species would be 20% lower. On the other hand, if toothfish consumption rate was doubled, as suggested by Longhurst & Pauly (1987), these values would double although this is unlikely as such a large change has not been detected (in CPUE for example). Adding additional species to the model or interactions between icefish and grenadier would also potentially influence model results.

## **Conclusions**

We have developed a spatially-resolved Minimum Realistic Model framework of the trophic interactions between toothfish and its two main prey species (grenadier and icefish) for the Ross Sea region. This model is resolved in space in cells of  $118 \text{ } 300\text{km}^2$ , which is similar to the scale of the management units (SSRUs).

Observed CPUE changes for icefish are consistent with the biomass changes expected by the model. This model captured the change in biomass of toothfish and its two main prey species in space, and accounted for biological parameters such as growth and recruitment of all species. The model also predicted changes in the diet of toothfish over time, due to the change in biomass of the prey species. Diet data and length frequency data did not show a statistically significant trend in the expected diet of toothfish or biomass of prey species with time due to the paucity of data available.

This model has proven useful in terms of framing predation hypotheses, with a Holling function being less likely than a predator-prey switch mechanism. It also provides an indication of potential changes in grenadier and icefish populations in the Ross Sea region. Such models can be developed in complexity, with the gradual addition of species of

importance to the toothfish diet, and their potential influence on the model results. However, in order to add other species, estimates of species distributions and ecological relationships are required. For example, grenadiers could be divided into *M. whitsoni* and *M. caml*, but this requires distribution data for both species, their relative biomass and the relative consumption of each by toothfish (Pinkerton et al. 2013). As a start towards this, observers should be asked to identify a number of grenadier bycatch per set to determine relative spatial distributions of the two grenadier species. Pinkerton et al. (Pinkerton et al. 2013) showed that CCAMLR/scientific observers are able to discriminate *M. whitsoni* and *M. caml* at sea using simple morphometric characteristics. Stomach sampling of toothfish should also continue, with grenadier in toothfish stomachs identified to species level where possible. Otoliths can be used for this purpose (Pinkerton et al. 2014b). Squid is another potential important prey species of toothfish, but its distribution, biomass or productivities are not known.

Models such as that developed here can be useful in assessing and designing monitoring tools for prey species, and for informing management decisions once models are validated. Results suggest that in order to be successful in monitoring prey species changes in time and therefore insure informed management decisions, length frequencies and diet composition studies should be carried out every few years with large sample sizes rather than yearly with low sample sizes. We recommend SSRUs 88.1H and 88.1K of the Ross Sea region are chosen as study areas with targeted sampling, as these are where the largest changes are expected to occur. Documenting the diet of toothfish along with length and otolith sampling of grenadiers and icefish should be carried out, with the aim to develop detailed diet composition estimates for toothfish through time and age frequency distributions of macrourid and icefish. This study could be carried out with high sampling intensity every 3–5 years.

## Acknowledgments

The authors would like to thank the scientific observers and fishers who collected the data used for this analysis. We would also like to thank the members of the New Zealand Antarctic Fisheries Working Group for helpful discussions and input into this paper. We thank the CCAMLR Secretariat for providing the data extracts and assisting in the interpretation of the data. This project was funded by the New Zealand Ministry for Primary Industries under project ANT2012/09, the Ministry of Business, Innovation & Employment (Project C01X1001, “Protecting Ross Sea Ecosystems” and Project C01X1226, “Ross Sea Climate and Ecosystems”), and the National Institute of Water & Atmospheric Research Ltd. (NIWA) under the Fisheries Centre Research Programmes 1 and 3.

## References

- Alaska Fisheries Science Center (2012). Attributes of the Eastern Chukchi Sea Food Web. 10 p.
- Begley, J. (2005). Gadget User Guide. [www.hafro.is/gadget](http://www.hafro.is/gadget). 95 p.
- Bury, S.J.; Pinkerton, M.H.; Thompson, D.R.; Hanchet, S.; Brown, J.; Vorster, L. (2008). Trophic study of Ross Sea Antarctic toothfish (*Dissostichus mawsoni*) using carbon and nitrogen stable isotopes. CCAMLR, Hobart WG-EMM-08/27. 41 p. Unpublished manuscript presented to the Ecosystem Monitoring and Management Working Group of CCAMLR.
- Christensen, V.; Walters, C.J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172: 109-139.

- Clark, M.R.; Dunn, M.R.; McMillan, P.J.; Pinkerton, M.H.; Stewart, A.; Hanchet, S.M. (2010). Latitudinal variation of demersal fish assemblages in the western Ross Sea. *Antarctic Science* 22(Special Issue 06): 782-792.
- Dunn, A.; Rasmussen, S.; Mormede, S. (2012). Spatial population model user manual, SPM v1.1-2012-09-06 (rev 4806). CCAMLR, Hobart WG-FSA-12/46. 164 p. Unpublished report presented at the Fisheries Stock Assessment Working Group of CCAMLR.
- Francis, M.P.; Gallagher, M.J. (2009). Revised age and growth estimates for Antarctic starry skates (*Amblyraja georgiana*) from the Ross Sea. *CCAMLR Science* 16: 211-220.
- Fulton, E.A. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems* 81: 171-183.
- Hanchet, S.M.; Mormede, S.; Dunn, A. (2009). Distribution and abundance of Antarctic toothfish in the Ross Sea. CCAMLR, Hobart WG-EMM-09/40. 25 p. Unpublished report held presented at the Environment Monitoring and Management Working Group of CCAMLR.
- Hanchet, S.M.; Mormede, S.; Dunn, A. (2010). Distribution and relative abundance of Antarctic toothfish (*Dissostichus mawsoni*) on the Ross Sea shelf. *CCAMLR Science* 17: 33-51.
- Hanchet, S.M.; Mormede, S.; Parker, S.J.; Dunn, A. (2014). The fishery for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *CCAMLR Science in press*.
- Hanchet, S.M.; Rickard, G.J.; Fenaughty, J.M.; Dunn, A.; Williams, M.J. (2008). A hypothetical life cycle for Antarctic toothfish *Dissostichus mawsoni* in the Ross Sea region. *CCAMLR Science* 15: 35-53.
- Heithaus, M.R.; Frid, A.; Wirsing, A.J.; Worm, B. (2008). Predicting the consequences of declines in marine top predators. *Trends in Ecology & Evolution* 23(4): 202-210.
- Holling, C.S. (1959). The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist* 91: 293-320.
- Horn, P.L.; Sutton, C.P.; DeVries, A.L. (2003). Evidence to support the annual formation of growth zones in otoliths of Antarctic toothfish (*Dissostichus mawsoni*). *CCAMLR Science* 10: 125-138.
- Jurado-Molina, J.; Livingston, P.A.; Ianelli, J.N. (2005). Incorporating predation interactions in a statistical catch-at-age model for a predator-prey system in the eastern Bering Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1865-1873.
- Longhurst, A.R.; Pauly, D. (1987). *Ecology of Tropical Oceans*, San Diego. 407 p.
- Mori, M.; Butterworth, D.S. (2004). Consideration of multispecies interactions in the antarctic: A preliminary model of the minke whale-blue whale-krill interaction. *African Journal of Marine Science* 26: 245-259.
- Mormede, S.; Dunn, A.; Hanchet, S.M. (2014a). A stock assessment model of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region incorporating multi-year tag-release and recapture data. *CCAMLR Science in press*.

- Mormede, S.; Dunn, A.; Hanchet, S.M.; Parker, S. (2014b). Spatially explicit population dynamics operating models for Antarctic toothfish in the Ross Sea region. *CCAMLR Science in press*.
- Palomares, M.L.; Pauly, D. (1998). Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research* 49: 447-453.
- Parker, S.; Grimes, P.J. (2010). Length and age at spawning of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. *CCAMLR Science* 2010: 53-73.
- Pinkerton, M.; Bradford-Grieve, J.M. (2014). Characterizing foodweb structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica. *ICES Journal of Marine Science*.
- Pinkerton, M.; McMillan, P.J.; Forman, J.; Marriott, P.; Horn, P.; Bury, S.J.; Brown, J. (2013). Distribution, morphology and ecology of *Macrourus whitsoni* and *M. caml* (gadiformes, macrouridae) in the Ross Sea region. *CCAMLR Science* 20: 37-61.
- Pinkerton, M.H.; Bradford-Grieve, J.M.; Hanchet, S.M. (2010). A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science in press (accepted)*.
- Pinkerton, M.H.; Bury, S.J.; Brown, J.C.S.; Forman, J.; Kilmnik, A. (2014a). Stable isotope analysis of tissue samples to investigate trophic linkages of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross and Amundsen Sea regionregions. CCAMLR, Hobart, Australia WG-EMM-14/xx.
- Pinkerton, M.H.; Ó Maolagáin, C.; Forman, J.; Marriott, P. (2014b). Discrimination of two species of grenadier (Gadiformes, Macrouridae), *Macrourus whitsoni* and *M. caml*, in the Ross Sea region of the Southern Ocean (CCAMLR Subareas 88.1 and 88.2) on the basis of otolith shape analysis. NIWA, Wellington, New Zealand NIWA report for NZ MPI.
- Punt, A.E.; Butterworth, D.S. (1995). The effects of future consumption by the Cape fur seal on catches and catch rates of the cape hakes .4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the cape hakes *Merluccius capensis* and *M-paradoxus*. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap* 16: 255-285.
- Punt, A.E.; Smith, D.C.; Koopman, M.T. (2005). Using information for 'data-rich' species to inform assessments of 'data-poor' species through Bayesian stock assessment methods. *Final Report to Fisheries Research and Development Corporation. Project no. 2002/094*. 243 p. Primary Industries Research Victoria, Queenscliff.
- Rassweiler, A.; Rassweiler, T. (2011). Does rapid scavenging hide non-predation mortality in coral-reef communities? *Marine and Freshwater Research* 62: 510-515.
- SC-CAMLR-XXXII (2013). Report of the thirty second meeting of the Scientific Committee. CCAMLR, Hobart, Australia.
- Secretariat (2013). Catches in the Convention Area 2011/12 and 2012/13. CCAMLR, Hobart, Australia. *SC-CAMLR-XXXII/BG/01*. 10 p.
- Shin, Y.-J.; Cury, P. (2004). Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 414-431.



Shurin, J.B.; Borer, E.T.; Seabloom, E.W.; Anderson, K.; Blanchette, C.A.; Broitman, B.R.; Cooper, S.D.; Halpern, B. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5: 785-791.

Stevens, D.W.; Dunn, M.R.; Pinkerton, M.H.; Forman, J.S. (2012). Diet of Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea region, Antarctica. CCAMLR, Hobart WG-FSA-12/52. 22 p. Unpublished report presented at the Fish Stock Assessment Working Group of CCAMLR.

Stevenson, M.L.; Hanchet, S.M.; Mormede, S.; Dunn, A. (2012). A characterisation of the toothfish fishery in Subareas 88.1 and 88.2 from 1997/98 to 2011/12. CCAMLR, Hobart WG-FSA-12/42. 38 p. Unpublished report presented at the Fish Stock Assessment Working Group of CCAMLR.

Sutton, C.P.; Manning, M.J.; Stevens, D.W.; Marriott, P.M. (2008). Biological parameters for icefish (*Chionobathyscus dewitti*) in the Ross Sea, Antarctica. *CCAMLR Science* 15: 139-165.