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Synthesis

How precautionary is the policy governing the Ross Sea Antarctic toothfish (*Dissostichus mawsoni*) fishery?

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Abstract: This article reviews the adequacy of data and models currently being used to estimate the present and future population sizes of the Antarctic toothfish (*Dissostichus mawsoni* Norman) in the Ross Sea regional ecosystem. The current tagging programme is unlikely to provide an accurate picture of total population size, and estimates of both the pre-exploitation spawning stock biomass and the ratio of current to pre-exploitation biomass are unreliable. Many parameters necessary for estimating future population growth or decline have not been measured, and the current objective of a 50% reduction in biomass relative to unexploited biomass may easily fail to prevent a much larger reduction from taking place. The need to guess values of important parameters makes it impossible to set bounds on the potential errors of population forecasts. Current scientific knowledge is far from what is needed to predict the likely effects of food-web responses to harvesting of toothfish in the Ross Sea, or to predict the feedback effects of those food-web changes on toothfish populations.

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Introduction

Sustainability is the core principle of most management plans for both conservation and exploitation of natural populations. Determining whether a course of action is likely to allow the persistence of a species or an entire biological community at healthy population sizes requires considerable knowledge about the population dynamics of those species. While there is a large body of scientific work directed at measuring and predicting the dynamics of fish populations (e.g. Hilborn & Walters 1992, Walters & Martell 2004), many observers have commented on the record of frequent failures in measurement and predicted futures of exploited fish populations (e.g. Ludwig 1998, Pauly *et al*. 1998, Hutchings & Reynolds 2004). This argues for a high degree of caution when initiating a new fishery on a species that is a major component of a unique ecosystem.

That describes the Ross Sea Antarctic toothfish (*Dissostichus mawsoni* Norman). Some aspects of the basic biology of this high trophic level notothenioid species are treated in Eastman & DeVries (2000), Fenaughty *et al*. (2003), Brooks *et al*. (2011), Parker & Grimes (2010) and Ashford *et al*. (2012). A hypothetical life cycle for the species is described in Hanchet *et al*. (2008). An exploratory fishery on Antarctic toothfish in the Ross Sea regional ecosystem was begun in 1996–97 under the direction of the Commission (CCAMLR) and Scientific Committee (SC-CAMLR) established by the 1982 Convention on the Conservation of Antarctic Marine Living Resources. This analysis focuses on the fishery in subarea 88.1, which constitutes the large majority of the current harvest, and is the area that has received the greatest amount of scientific study. However, most of the following is likely to apply equally well to the adjacent subarea 88.2, as well as other exploratory fisheries in the Antarctic that capture *D. mawsoni* (subareas 48.4, 48.6 and 58.4; see SC-CAMLR 2012), for which much less is known about the fish population. Recent reports of the SC-CAMLR Fisheries Stock Assessment (FSA) working group (SC-CAMLR 2011 Appendix R and SC-CAMLR 2012 Appendix N describe the basis of the CCAMLR intent to continue the current harvest of *D. mawsoni* in subarea 88.1 (with the previous quota of 2850 tonnes per year increased to 3282 tonnes in 2012). Amounts similar to the suggested quota have been harvested each year in the area over the period 2001–02 to 2012–13 under the 'exploratory' fishery. Both the 2011 and 2012 reports estimate that this harvest level will reduce the standing stock biomass to one-half of its unexploited level over a 35-year period. They also conclude that the current harvest policy will incur a <5% probability of reduction of the population to one-fifth or less of the unexploited biomass. These documents argue that the proposed 50% reduction is a precautionary level of harvesting for the species (see also Constable *et al*. 2000). The current quota and associated management plan have resulted in certification of the fishery as sustainable by the Marine Stewardship Council, an organization that has recently been the subject of a favourable review by a group of fisheries biologists (Gutierrez *et al*. 2012, see Christian *et al*. 2013 for a critical review). The fishery was also recently endorsed as a 'good alternative' by the Monterey Bay Aquarium's Seafood Watch programme, which ranked the fishery in its highest category for its low impact on the stock and good management plan. Nevertheless, many marine ecologists have expressed opposition to the management plan (Blight *et al*. 2010, Ainley & Pauly 2013, O'Brien & Crockett 2013). The question addressed here is whether current knowledge of stock size, population dynamics, and ecosystem interactions justifies the apparent confidence of at least the CCAMLR and SC-CAMLR fishery scientists in the sustainability and lack of adverse ecosystem impacts from the current harvest policy. While questions about this management plan have already been raised, as noted, a number of the points presented below do not seem to have appeared in the previous literature. Although some ecological unknowns exist for most fisheries, there are some particularly large gaps in current understanding of *D. mawsoni* dynamics, and a larger potential for negative consequences from overharvesting.

Current knowledge of population size

The need for a more precautionary approach stems from the lack of knowledge of the current and recent population sizes of Antarctic toothfish and of the mechanisms regulating future population growth. The population size estimates used in Appendices R and N are based upon a very limited time series of returns from an exploratory fishery, supplemented by limited tagging and recapture studies carried out on fishing vessels. The population biology of the first 10 years of life is almost completely unknown. Current population size and the likely response of the population to the on-going harvest are therefore highly uncertain.

Present estimates of population size are based on tagging that began in 2001–02, but relatively few fish were tagged during the first 3 years of the programme. Systematic tagging began in the 2005–06 season. Appendix R restricted the analysis to a subset of vessels and trips that met certain data quality standards. Based on these data, recovered tags first exceeded ten individuals in 2005, and the analysis was based on the total of 474 recoveries (of 13 308 tags), almost all of the recoveries taking place in the period from 2005 until the end of the season in 2009 (Appendix R table 10). Large numbers of recoveries in 2010 and 2011 combined with reclassification of earlier data in the 2012 report (Appendix N table 10a) raised these totals to 859 and 19 514 respectively. In comparison, the programme undertaken to estimate cod (*Gadus morhua* L.) exploitation rates off the north-east coast of Newfoundland (in 1997–2002) involved tagging over 26 000 fish, with nearly 4000 recoveries by 2003 (www.dfo-mpo.gc.ca/csas-sccs/publications/resdocs-docrech/2003/2003_032-eng.htm). This much larger programme, independent of fisheries vessels, has still not provided a basis for agreement on current densities or harvesting regulations (Hutchings & Rangeley 2011).

Mark-recapture based estimates of population size require assumptions about lack of variation in survival, random spatial mixing, behavioural homogeneity, lack of behavioural changes caused by capture/tagging events, and matching spatial distributions of sampling and the sampled population. The average individual properties may differ between sexes and age/size classes, and, if potentially significant in magnitude, these differences should be known. There are many gaps in the Ross Sea data, which cause problems for the population size estimates. Both fish mortality rates and the movements of fish relative to vessels have significant uncertainties. Mortality rates appear to be based on observed size structure of captured fish (Dunn *et al*. 2006), which also creates a number of uncertainties. All tagging was done on fishing vessels, which are limited by CCAMLR regulations to longlines at depths > 550 m, and which concentrate their effort where catch rates have proved to be the highest (Ross Sea slope, depths 800–1200 m; Hanchet *et al*. 2010). This means that the spatial distribution of tagging and recovery effort was unlikely to match that of the population. The nature and consequences of these mortality and movement uncertainties are discussed below.

The description of population size estimation in Appendices R and N are essentially the same as those in Dunn & Hanchet (2010). This involves using a computer program to fit a simple size-structured population model to the catch and tagging/recovery data, by minimizing an objective function reflecting differences between observed data and model predictions. Their method generates surprisingly narrow confidence intervals for the estimates of population sizes. For example, Appendix R (p. 23) gives an estimate of 2009 biomass as 49 580 tonnes with 95% confidence intervals of 12.2% below that figure (43 530) to 16.3% above that figure (57 670). More surprisingly, Appendix R asserts that this biomass in 2009 was 79.9% of the pre-fishing biomass, with 95% confidence intervals of 77.7–82.2%. The 2012 update (Appendix N) claims, with two more years of data, that the 'current' (unclear if it is 2011 or 2012) proportion of biomass remaining is larger, 80.0%, with still narrower 95% confidence intervals of 78.6–81.3%. The projected 1.5% annual decline due to harvesting (Appendix N) should have changed the 79.9% estimated reduction in 2009 to 76.9% in 2011, but the latter figure is significantly below the lower confidence bounds for 'current'. The estimate of current Ross Sea biomass in 2012 (Appendix N), 59 110 tonnes, is 1440 tonnes greater than the upper 95% confidence interval for the 2009 population given in the 2011 SC-CAMLR report. The estimated original ('Ross Sea base case') biomass from 2012 (73 870) exceeds the upper 95% confidence interval for that original biomass estimated in 2011 (70 090). Perhaps the 2012 figures are more accurate, but the contrast certainly casts great doubt on the 95% confidence intervals in both reports, which are based on essentially the same methods. In fact, outright assumptions of several key relationships and parameters make all of these estimates and their confidence intervals questionable.

The survival rate of tagged individuals is important for estimating biomass. Appendix R (SC-CAMLR 2011) sets the mortality rate during tagging as 10%. If 20% of tagged individuals die due to tagging within a year of being marked, the number of tags present in future years will be overestimated by approximately 10% and the population size estimate will be too high by approximately the same amount. However, the basis provided for the 10% figure in Dunn & Hanchet (2010) is that 10% is double the estimate in a study (Agnew *et al*. 2005) of a related species (*D. eleginoides* Smitt). The latter study measured survival over 12 hours in holding tanks on fishing vessels following capture and tagging. This fails to account for mortality due to post-release predation or infections, both potential causes of mortality in recently released tagged individuals. The method also ignores slow starvation (or increased predation risk over a longer time period) due to jaw or neurological damage (injuries to the jaw were noted frequently in Agnew *et al*. 2005). Differences in the species, the size distribution, the tagging technique, the conditions on the vessel and other factors could also mean differences in survival of tagged *D. mawsoni*. The finding of a recently tagged *D. mawsoni* in the stomach of a larger individual (Petrov & Tatarnikov 2010) shows that predation is indeed a possibility. (See also the comment about small hooked fish being wounded by large fish in Ainley *et al*. 2012.) A tagging-related mortality of 20% is just as likely as the 10% assumed, and this alone would put biomass estimates well outside of the 95% confidence intervals, assuming all other parameters were accurately and precisely estimated.

The estimate of natural mortality also affects the population size estimate by determining number of surviving tagged individuals. The figure for natural mortality used in Appendices R and N projections was proposed as a possible value of natural mortality for *D. eleginoides* in 2006 (Hillary *et al*. 2006) based on the idea of life-history invariants (Charnov 1993). These 'invariants', however, are only rough correlations between pairs of life-history traits evident in very large sets of species, so they provide a very weak basis for estimating those trait values in any particular species. A later estimate of natural mortality based on size/age structure (Dunn *et al*. 2006) curiously came up with exactly the same figure for *D. mawsoni*, and that figure was adopted in the Appendices N and R analyses. Dunn *et al.* (2006) estimated a single natural mortality for all individuals using both Chapman-Robson (1960) and Hoenig (1983) methods (as well as an unpublished modification of the Hoenig method by Andre Punt). All of these depend on accurate assessment of age structure and the assumption of a stable age distribution with equal mortality across age classes. The Chapman-Robson method, as applied by Dunn *et al.* (2006), is based on average age above the age at which all fish are vulnerable to sampling. Hoenig's method and its variants are based on the minimum age of the oldest 1% of the sample. The observed age distributions are confounded in unknown ways by potential differences in size- and age-specific probabilities of capture. Extreme value statistics, such as the maximum age figure in Hoenig's method are extremely sensitive to sample size, and could easily be too high if there are significant increases in mortality associated with senescence. Furthermore, mortality is usually a function of age and size, and often sex. An attempt to measure natural mortality in the Heard/McDonald Island populations of *D. eleginoides* by Candy *et al.* (2011) resulted in an estimate of 0.155 with wide 95% confidence intervals (0.055–0.250). While it is uncertain how confidence intervals can be determined for figures based on so many unverified assumptions, it is likely that the uncertainties in *D. mawsoni* natural mortality are comparable to those reported by Candy *et al.* (2011). Such uncertainties would be sufficient to alter population size estimates by more than a few percent.

Assumptions regarding behaviour and movement could result in much larger errors in population size estimates than assumptions about mortality rates. Increased avoidance of longlines following capture, tagging and release would inflate the population size estimate but nothing is known about this possibility. Movement of individuals out of the area where fishing vessels operate would reduce recapture probability, and would again increase population size estimates. This seems likely for larger individuals, which must travel long distances to the putative spawning grounds (Petrov & Tatarnikov 2010, Ashford *et al*. 2012). Smaller individuals are negatively buoyant and appear to move relatively little. However, lack of fish movement can also result in overly large population estimates if the fishing vessels move moderate distances from year-to-year to avoid locations that have been depleted by fishing of sedentary individuals in the previous year(s). This again reduces tag recovery rates (and inflates population size estimates) relative to the ideal assumptions of random sampling across the entire range by humans and rapid random movement by fish.

Movement, as well as nearly everything else about young fish is unknown, as they are virtually absent from the catch (SC-CAMLR 2011, 2012). The analysis by Ashford *et al.* (2012) of otolith chemistry supports a common spawning area for the entire population. The exact location is as yet unknown, eggs and larvae have not been observed, and subsequent movements of individuals to/from supposed spawning grounds (seamounts north of the Ross Sea; Hanchet *et al*. 2008) have not been documented directly.

Uncertainty about fish movement also affects the interpretation of likely future temporal changes in tag returns. If fish occur in spatially heterogeneous environments that differ in resource productivity, correlated movements of fish (towards the most productive areas) and vessels (to areas with more fish) obscure population declines. It appears that a lack of awareness of this type of correlated movement was a major factor in the lack of warning of the decline of Atlantic cod (*Gadus morhua*) during the decade preceding the collapse (Hutchings 1996). Such correlations can lead to abrupt collapses of the population (Abrams *et al*. 2012)

Estimates of pre-harvesting biomass are also particularly problematic, as there was no survey programme that preceded fishing. The Dunn & Hanchet (2010) approach used by SC-CAMLR (2011, 2012) is based on fitting population sizes to a population dynamics model that assumes a constant environment, with the only change in recent years being the addition of fishing. The recent population estimates fix the pre-harvest population at a level slightly higher than that estimated for the first few years of harvesting. A meaningful estimate of baseline population size would also have to consider population variability, as we have no idea whether the toothfish population at the year immediately before the start of the fishery (1997) was anywhere near the average for the twentieth century, or even for the last few decades of that century.

In summary, the claims that the current population size of *D. mawsoni* is known to within 10–15%, and the extent of current fractional reduction from baseline to within 1–2% are insupportable given that: i) the effective number of years of tag recoveries is less than the time required for a female to reach maturity (Parker & Grimes 2010), ii) both tagging and recovery have been carried out only on fishing vessels and only in a small part of the habitat used by the species, iii) movement patterns of fish and boats relative to fish are very poorly known, iv) the natural variation in the size and composition of the unharvested population is completely unknown, and v) the estimated post-tagging mortality rate is based on a figure for another species which, even for that species, lacks any consideration of increased predation and disease risk of tagged individuals. All of these limitations introduce potential errors whose size could be extremely large, but cannot meaningfully be estimated, given the data described in those articles. The narrow confidence intervals in published work reflect an unrealistic approach to estimating uncertainties.

Lack of knowledge of population dynamics

Projecting future population sizes over a significant time interval requires some knowledge of the direct and indirect effects of population size on the per individual birth minus death rate, as well as what those rates are currently. There is presently no evidence with which to estimate the effects of density dependence on vital rates in Antarctic toothfish. The dogma in fisheries is that density dependence primarily affects reproduction and/or juvenile survival, leading to a stock-recruitment relationship. Unfortunately there are no data that can be used to determine such a relationship for *D. mawsoni*, given that most individuals caught in the Ross Sea regional fishery after 2003 are 10–15 years of age (Ashford *et al*. 2012 fig. 5) and, thus are late-stage pre-recruits. The estimated modal age of maturity is 12.8 for males and 16.6 years for females (Parker & Grimes 2010, Appendix R). The lack of data on small individuals means that we have very little direct information on the reproductive rate or the stock-recruitment relationship, let alone the effect of fishing on recruitment. Male *D. mawsoni* that hatched when the reported catch approached its current target level (2002–03) are just now beginning to attain reproductive maturity, the average female will not do so for another 6 years according to the modal life-history parameters cited above. Even then, the first few recruits will only have experienced significantly reduced density in the latter part of their juvenile period. There has been an initial attempt to census smaller pre-recruit size classes using a chartered commercial fishing vessel (www.niwa.co.nz/news/survey-reveals-plenty-of-fish-in-the-ross-sea). This document indicates that a regular survey would be proposed at the next FSA working group meeting. Few details about the survey that was undertaken are given, although fish in the 70–100 cm length class are described as abundant. This is consistent with previous catches on the southern shelf (cf. Ashford *et al*. 2012). The size distribution in this new survey is similar to that sampled in 1999–2003 (SC-CAMLR 2012). The nearly linear length *vs* age relationship that is likely to be found in the juveniles of most long-lived fish (Quince *et al*. 2008) combined with the Appendix R estimates of age at maturity indicates that the 2012 NIWA survey sample consists of fish that are at least 8–10 years old (cf. Brooks *et al*. 2011). Thus, they still do not provide a basis for detecting any effect of fishing-caused changes in spawning stock biomass on recruitment.

The population projections described in Appendices R and N were made using a Beverton-Holt stock-recruitment relationship with a steepness parameter of 0.75 and log-normally distributed variability in recruitment having a standard deviation of 0.6. All aspects of this projection scheme are based on assumptions rather than data for *D. mawsoni*, and the reasoning underlying those assumptions is not laid out in the two reports. These two parameter values are similar to the mean values in a collection of stock-recruitment data by Myers *et al*. (1999), and this similarity was used to justify these figures in Dunn *et al*. (2006), which appears to be the original source of these assumptions for Appendices R and N. However, this does not mean that these average values will be anywhere close to the best-fit values for *D. mawsoni*, should data become available to determine them at some future time. Nor is there any evidence to judge the applicability of the Beverton-Holt form of the relationship.

Unintended overexploitation of many other fish stocks has occurred in spite of a much longer history of exploitation, more extensive and fisheries-independent efforts to monitor population size, and more complete knowledge of population dynamics, including recruitment rates of small individuals (Longhurst 2010). Hutchings & Reynolds (2004) provide a general review of the many previous cases of overexploitation. Hutchings & Myers (1994) analyse the role of exploitation in the collapse of the comparatively well-studied northern Atlantic cod, a population that had been heavily exploited since 1860 and studied intensively for several decades before the collapse. A great deal of data existed on stock size and recruitment but uncertainties about this relationship permitted harvesting levels that collapsed the stock. The durations of both harvesting and programmes to estimate population sizes of Antarctic toothfish are brief in comparison.

As a result of the limited time-span of population data, there is also no evidentiary basis for estimating a low-density growth rate for Antarctic toothfish, as low spawning stock biomass relative to the un-fished state has not occurred during the period which has been studied. Some knowledge of the stock-recruitment relationship and low-density rate of increase (or more generally, density dependence) are essential aspects of any single-species approach to modelling population dynamics. Such knowledge is obviously essential for estimating the biomass that produces maximum sustainable yield (MSY). Understanding density dependence is thus required to design regulations that ensure sustainable harvesting, and to estimate the risk of population collapse and the probability of recovery following such an event. Hutchings (2001), Hutchings & Rangeley (2011), and Keith & Hutchings (2012) have argued that lack of data from significant periods of low-stock abundance is a more general problem with the use of current stock-recruitment data to estimate parameters in hypothetical stock-recruitment relationships. There are strong reasons for believing that recruitment processes may change qualitatively after a significant period of greatly reduced stock biomass (see also Neubauer *et al*. 2013).

Possible ecosystem responses

A basic problem with the traditional single-species approach used in the SC-CAMLR analyses is that the population dynamics of almost all fish species are determined by its food resources, predators and environment (i.e. by the rest of the ecosystem) than by its current population density. A multi-species or 'ecosystem' approach to fisheries management has now been widely endorsed (Link 2010), even by previous critics (cf. Walters & Martell 2004 to Hilborn & Walters 1992). It is mandated by the Article II objectives of the CCAMLR, and has been endorsed for analyses of the Antarctic system generally, although not for toothfish (Constable *et al*. 2000). The lack of both basic theory and empirical studies has delayed effective implementation of such an approach for toothfish. Moreover, even the attempted use of multi-species approaches in the Antarctic toothfish system has largely been restricted to estimating the impact of the *D. mawsoni* fishery on other species in its food-web. However, the ecosystem also determines the form of density dependence experienced by a high trophic level predator like adult *D. mawsoni*, and simple food-web models show that traditional stock-recruitment models cannot reflect a large fraction of the range of possible relationships (Abrams 2009a, 2009b, Tschirhart 2012). Hill *et al*. (2008) argue that the uncertainties of ecosystem model structure call for analyses of a variety of models, a theme re-emphasized for the Southern Ocean by Murphy *et al*. (2012). Analysis of multiple models is a good approach in theory, but its value depends on the range of models being a good reflection of the potential range of biological reality. There is no evidence that enough is known about the role of toothfish in the Antarctic marine ecosystem to narrow the range of potential models to a manageable number that includes all plausible ones. A frequently used alternative to the 'many models' approach under ecosystem-model-based management is to employ computer packages designed for marine fish communities, such as Ecopath with Ecosim (Christensen & Walters 2004); this usually involves accepting an order of magnitude more assumptions about unknown quantities than do the single-species models.

Even in the absence of a full ecosystem model, accounting for the strongest interacting members of the biological community should improve population projections for a species of interest. Such 'strong interactors' must form the backbone of a full ecosystem model. If this more limited multi-species approach is not possible, then a predictive ecosystem model is out of the question. Predators and food species are the main factors involved in producing density dependence in fish. If all density dependence in *D. mawsoni* arose from predation and cannibalism of eggs and larvae, something would have to be known about these processes to deduce a stock-recruitment relationship. Unfortunately, nothing is known about the early life-history stages of *D. mawsoni*. Moreover, it is evolutionarily unlikely that density dependence should be restricted to a single life stage. As a large predator, it seems likely that density dependence in adult *D. mawsoni* arises at least partially from either depletion of prey or shifts in the composition of the prey to less nutritious and less catchable types as the toothfish becomes more abundant. The general range of impacts of these food-web processes on the regulation and dynamics of a predator population have been discussed (Abrams 2009a, 2009b). These studies suggest that a wide variety of relationships between standing biomass and yield are possible, and that many plausible assumptions lead to dramatic decreases in equilibrium yields over a small range of harvest rates that are only slightly above the MSY rate (Abrams 2009a, 2009b). The general consumer-resource models analysed in these studies indicate that equilibrium stock sizes close to 20% of the unexploited size frequently entail exploitation rates only marginally below rates which, if sustained over time, would cause extinction.

If food is the main source of density dependence in a predatory species, then knowledge of the predator's functional and numerical response shapes, plus the resource populations' dynamics (density dependence and interactions) and nutritional qualities are required to determine what level of exploitation maximizes yield and how abundance shifts with greater or lesser exploitation (Abrams 2009a, 2009b). Furthermore, translating such information into relationships between harvest and equilibrium abundance would also require a breakdown of many of the species into size or age classes. In addition, the seasonal and spatial changes in diet need to be understood. Although there have been studies of *D. mawsoni* diet (Eastman 1985a, 1985b, Fenaughty *et al.* 2003, Hanchet *et al.* 2003, Stevens 2004, Roberts *et al.* 2011, Stevens *et al.* 2012), all of these are restricted in terms of location, size classes, or time-of-year, and all except Eastman (1985a, 1985b) involve only fish from the continental slope or seamounts. Diet in the shelf study was dramatically different from that over the slope. Only Stevens *et al.* (2012) combine diet determinations with measurements of prey abundance to quantify predator functional responses to different prey species. However, even in this study, the fact that only catch per unit effort (CPUE) data were used to estimate prey abundance lends a high degree of uncertainty to the resulting functional response estimates. While grenadiers (*Macrourus* spp.) have been identified as the most abundant prey in more than one deep water (seamount or slope) study, cephalopods are frequently reported in toothfish stomachs from those areas, as well as a variety of other fish species and invertebrates. Stevens *et al.* (2012) found higher selectivity for fish species that were less represented in the diet. Moreover, the diet of *D. mawsoni* caught in the water column over the shelf, which includes mostly sub-adult individuals, appears to be dominated by the mid-water prey species, *Pleuragramma antarcticum* Boulenger (Eastman 1985a, 1985b, Fenaughty *et al.* 2008). Euphausids (*Euphausia superba* Dana or *E. crystallorophias* Holt & Tattersall), are a potentially important component of the diets of both small and large *D. mawsoni* (LaMesa & Eastman 2012, Fenaughty *et al.* 2008). The diet is sufficiently diverse that it would be difficult to deduce how changes in *D. mawsoni* would affect its food supply. The migratory life history of this species (Hanchet *et al.* 2008, Ashford *et al.* 2012) with different food sources in different places is likely to increase the possibility of alternative equilibrium states and abrupt changes in population size in response to continuous environmental change (Schreiber & Rudolf 2008).

Other aspects of the relationship of *D. mawsoni* to its food-web are also poorly known. It is not known whether post-spawning fish recover their fat-depleted condition in the food-sparse ocean waters where they are thought to spawn. Switching the ecological role of toothfish, the effect of mammalian predators (toothed whales and seals), both in producing mortality and in limiting foraging times and locations, has yet to be studied. Given that *D. mawsoni* is likely to be one of the two most important fish prey species of large predatory mammals in the Ross Sea region (Testa *et al.* 1985, Ainley & Siniff 2009), it is probable that higher-level predatory influences on toothfish dynamics are substantial. Predator avoidance behaviour and predator-driven dispersal can greatly change population dynamics in theoretical and experimental systems (Werner & Peacor 2003, Abrams 2010). The importance of such behaviourally mediated effects has been recognized (Ahrens *et al.* 2012). Everson (1970) provides one of the first descriptions of shifting habitat use driven by seal predation in an Antarctic fish (*Notothenia neglecta* Nybelin), and Alonzo *et al.* (2003) argue that predator avoidance by the diel vertical migration of krill has a major effect on their dynamics in the Antarctic ecosystem. A complete lack of knowledge of similar potential non-consumptive effects of predators on or prey of *D. mawsoni* makes it difficult to justify any particular family of food web models to guide harvesting. All of this implies that we are far from being able to construct a predictive model of the dynamics of Antarctic toothfish that incorporates realistic descriptions of its most important and direct food web interactions.

The above considerations have not prevented attempts to model the food-web (or ecosystem) of the Ross Sea (Pinkerton *et al.* 2010) using Ecopath with Ecosim (Christensen & Walters 2004). Applications of this package in the fisheries literature have increased rapidly since its introduction, but this has not been accompanied by either general acceptance of Ecosim in the broader ecological community or critical examination within the fisheries community. The constantly changing nature of the program makes critical analysis of the models difficult. However, analyses of explicit food-web models have shown that such unknown functions as size-specific growth rates, consumer functional responses, and the presence and nature of adaptive changes in foraging can all have dramatic effects (e.g. de Roos & Persson 2002, Abrams 2010). Ecosim assumes a functional response formula with strong negative effects of consumers on their own responses (Christensen & Walters 2004). This greatly reduces the possibility of consumer extinctions and reduces the magnitudes of trophic cascades and other indirect effects. There are qualitative uncertainties about toothfish diet, and essentially no direct information bearing on functional responses. The functional form of population dynamics models for one of the most important Antarctic populations (krill) still involves major unknowns (Atkinson *et al*. 2012). As a result, the conclusions of the analyses of the 35-component computer models described by Pinkerton *et al*. (2010) should be viewed with caution.

Does reduced harvesting following a one-half reduction in stock size provide reasonable insurance against a collapse?

Because the conclusions reached here are at odds with various international assurances of sustainability, it is worthwhile addressing the reasons for this difference. The positive assessments seem to be based on the assumptions that the target level of exploitation is relatively low and that population size assessments will allow adjustment of quotas in time to halt unanticipated declines in the population. If the procedures for estimating toothfish population size were improved it might be possible to place more confidence intervals on the estimates. If this occurs, and if harvesting is reduced or temporarily stopped when biomass drops below one-half of the estimated pre-exploitation biomass, will this ensure the continued existence of a healthy population? In the recent literature (e.g. Hilborn 2010, Hilborn & Stokes 2010), it is commonly assumed that maximum sustained yields are usually attained at biomass levels that are significantly less than one-half of the unexploited level. For example, Hilborn (2010) shows that yields close to the optimum most often require that populations be below 60% of their unharvested abundance, and are usually attained when the population is in the range of 20–25% of unharvested abundance. This might be seen to imply rapid regeneration from even one-quarter of pre-exploitation biomass and makes a reduction of 50% seem like a relatively conservative target. However, the Beverton-Holt relationship itself is an assumption for almost all fisheries, with existing data being consistent with a wide variety of other relationships (e.g. Ludwig 1998), and the parameter values of the best-fit Beverton-Holt relationship are highly uncertain. Analyses of such existing stock-recruitment data have shown that data from low stock abundance are frequently sparse (see below) and, when available, generally exhibit much greater variability than at higher stock sizes (Myers 2001). This variability is what would be expected if community responses to low stock densities of the focal species were important determinants of its rate of increase from those densities. Maximizing temporal average yields in fluctuating environments (i.e. all real environments), generally requires harvesting at rates considerably below the MSY-point of the corresponding deterministic model (Ludwig 1998). Fluctuations in many Ross Sea environmental variables have been particularly large in recent years (Stammerjohn *et al*. 2012). Maximizing yields in models where the food supply of the harvested species determines reproductive rate often entails MSY at populations much greater than 50% of unexploited biomass, even in constant environments (Abrams 2009a, 2009b).

There are reasons for suspecting that single-species models are likely to underestimate the risk of collapse posed by high levels of harvesting of large predatory species in a food-web. Food-web models of predators at high trophic levels whose young have different diets often exhibit two or more equilibria or attractors and the presence of abrupt changes that are irreversible on a short timescale. Such outcomes have been described in different models by Walters & Kitchell (2001), de Roos & Persson (2002) and Abrams (2011). A common mechanism producing an alternative state with few or no predators is that depression of predator populations allows increases in the size and/or numbers of prey, which then have adverse effects on juvenile predators (either via competition with or predation on the juveniles). This is not a purely theoretical result. It is one of the main explanations proposed for the non-recovery of cod stocks in the north-west Atlantic (e.g. Swain & Sinclair 2000, Swain 2011), and it could easily apply to *D. mawsoni*. Hutchings (2000, 2001) catalogues a variety of stocks that have failed to recover following population reductions due to fishing despite drastic declines in harvesting (Longhurst 2010). This is inconsistent with the single-species Beverton-Holt relationship, but is expected when shifts in food-web structure brought on by heavy exploitation of adults of a large predatory species produce decreased per capita growth rates, due either to changes in population structure or food-web interactions. Keith & Hutchings (2012) found evidence of such low population traps for heavily exploited Canadian cod and Alaskan Walleye Pollock (*Theragra chalcogramma* (Pallas)). They also suggest that one-third of the species in the Myers database exhibit no evidence of density compensation (higher per capita growth at lower densities) when the analysis is restricted to species that have experienced low standing stock biomasses. Hutchings & Rangeley (2011) conclude that 'Emergent and demographic Allee effects, coupled with altered interspecific interactions, render questionable the presumption that the recovery of heavily depleted populations can be reliably forecasted by population dynamical behaviour during the decline.' While higher target abundances reduce the possibility of collapse due to food-web shifts, the nearly complete lack of quantitative knowledge of predator-prey relationships in the *D. mawsoni* food-web makes it impossible to estimate the density at which such regime shifts might become possible.

The possibility of regime shifts also places limits on the use of adaptive management and knowledge of population size to ensure against collapse of a target population, even if population size were known accurately. Regime shifts can in theory be triggered by either harvesting or environmental change. Because we do not know the range of historical densities of *D. mawsoni*, or the point at which a major food-web shift might occur, even accurate knowledge of current densities is unlikely to provide warning of a collapse due to a harvest-driven regime shift. Environmentally driven regime shifts on a decadal scale have been described for the Southern Ocean (Dayton 1989, Jenouvrier *et al*. 2005). The possibility of decadal changes in food availability was proposed as one possibility to explain long-term changes in the condition of toothfish caught in McMurdo Sound (Ainley *et al*. 2012). La Mesa & Eastman (2012) suggest that climate change could easily collapse the population of *Pleuragramma antarcticum*, which is a key food source for *D. mawsoni*, at least over the shelf.

Other complications for population projection

Spatial structure in the environment combined with movement of individuals can greatly alter population dynamics, and it is well known that *D. mawsoni* can travel thousands of kilometres (Eastman & DeVries 2000, Hanchet *et al*. 2008, Petrov & Tatarnikov 2010). Recent work (Ashford *et al*. 2012, Hanchet *et al*. 2008) argues that *D. mawsoni* in the south-east Pacific Basin and Ross Sea is likely to constitute a single population with spawning most likely among the seamounts north of the Ross Sea slope, and subsequent dispersal to other areas driven by currents. Nevertheless, details of the movements are largely unknown. This complicates the use of mark-recapture techniques to monitor population size. It also means that exploitation of fish across part of the range may provide a misleading estimate of total population size and/or productivity, as a significant input to the fishery in early years may well come from immigration rather than reproduction. Theoretical models (Abrams *et al*. 2012) have shown the potential for abrupt population collapse with increased harvesting in a system having spatially heterogeneous harvest combined with food-based habitat choice by the harvested species. If an abrupt collapse in adult densities occurs, the lengthy juvenile period for *D. mawsoni* and the fact that spawning is not likely to be annual (Parker & Grimes 2010, Ashford *et al*. 2012) will prevent rapid recovery.

Other mechanisms can delay the recovery of overexploited stocks. Adaptive evolutionary shifts in life-history traits of the exploited species are possible (e.g. Heino & Godø 2002, Walsh *et al*. 2006, Longhurst 2010). There is also evidence from some species that shifts to a smaller and younger average female size can affect egg quality as well as reproductive output (Berkeley *et al*. 2004). Neither of these mechanisms appears to be included in the models used to estimate the maximum sustainable harvest of *D. mawsoni* (Appendices R and N). Either could produce a lower than desired stock abundance that could persist for many generations despite reduced harvesting (Shust & Kozlov 2006).

In many systems illegal fishing is a problem, and Appendix R lists some IUU (illegal, unreported and unregulated) catches of *D. mawsoni*. It is difficult to judge the extent of illegal fishing in the Antarctic, although the extreme environment provides some protection, and the presence of observers on all licensed boats presumably ensures compliance. On the other hand, by its nature IUU fishing is extremely difficult to quantify. Its level is thought to be low in the Ross Sea region but high in neighbouring waters (Österblom *et al*. 2010, Ainley & Pauly 2013). The fact that the currently established quota can be caught legally, both in the Ross Sea and waters to the west, within one month (as has been the case in recent years) indicates that significant biomass could be caught illegally over a very short time period. Indeed, an illegal 130 km long gillnet with 29 tons of *D. mawsoni* was recovered off East Antarctica in 2009 (www.traffic.org/home/2009/11/6/australia-confiscates-130-km-long-deepwater-gillnet.html). The ability to rapidly capture large quantities of fish makes detection of illegal activities more difficult (and adds to the general problems of monitoring such activities in remote areas likely frequented by the Ross Sea stock). In several other important fisheries, IUU catch has been estimated to exceed 30% of total catch (Doulman 2001). Mortality due to unreported catch and discarding of small individuals likely contributed to the Atlantic cod collapse (Myers *et al*. 1997). Mortality of discarded individuals and individuals that sustain injuries freeing themselves from longlines could have a large effect on a species like *D. mawsoni*.

While the above analysis is based on analyses of populations in the greater Ross Sea area, much of it is likely to apply to other *D. mawsoni* populations, some of which have had or may in the future have exploratory fisheries (Ainley & Pauly 2013). A number of the above criticisms of *D. mawsoni* fishery practices apply to many other currently exploited fish species that lack a long history of either harvesting or research. This certainly includes many populations of the Patagonian toothfish (*D. eleginoides*) in the Antarctic and elsewhere. The possibility of over-exploitation of Ross Sea Antarctic toothfish is particularly high for several reasons. There is far less of a historical record of exploitation and its effects, as there was no commercial fishing prior to 1997. The long juvenile period combined with the short history of the fishery means that there is no knowledge of the effects of density on recruitment. This long juvenile period combined with the current inability to census fish during their first decade of life means that a collapse of recruitment would be likely to remain hidden for a decade. Efforts to reverse such an event would then require another decade before increases in newborns translated into an increase in the spawning stock, even if reduced fishing was immediately successful in raising the birth rate. Because of its lack of anti-freeze and the fact that it is also subject to the same forces promoting exploitation, Patagonian toothfish (*D. eleginoides*) populations are unlikely to increase and substitute for the Antarctic species in the functioning of the Ross Sea ecosystem.

The Antarctic environment, and especially that of the Ross Sea region, is undergoing extreme and rapid alteration in the ice environment (Stammerjohn *et al*. 2012). It would be surprising if this did not have major effects on the food web in which *D. mawsoni* is embedded, which would then affect maximum harvest rates as well as the entire production-harvest relationship. For example, the eventual predicted loss of ice cover over increasing areas and time periods could greatly increase predation rates by mammals (whales and seals); habitat selection by *D. mawsoni* to reduce predation risk in turn could diminish their food intake and growth rates. Increases in ice cover over the shorter term could have the opposite effects in some areas, including the Ross Sea, where such increases have occurred in recent decades (Stammerjohn *et al*. 2012). However, the time course and ultimate extent of such changes cannot be predicted with any accuracy at present. The fact that very significant environmental changes are likely within a time span equal to two generations of the harvested species means that population growth parameters estimated using data from one decade may well be inaccurate in the next.

Conclusion

All of the above reinforces the message that an approach to harvesting *D. mawsoni* that is more conservative than the current policy is called for, at least until much more is known about this species' population biology. More broadly, the fact that the current fishery for this species has been labelled 'sustainable' by the Marine Stewardship Council and a 'good alternative' by Seafood Watch calls into question current criteria for positive ratings by the groups likely to have the largest impact on consumer decision-making. The possibilities for negative outcomes described above are not certainties. However, they are no more hypothetical than are the population projections of the SC-CAMLR (2011, 2012) reports. Given the scientific value of intact and relatively pristine polar ecosystems, the lack of benefits of cultural preservation or human nutrition from the fishery, and the inability of the vast majority of the world's population to afford purchase of the fish, the balance of risks and benefits of a *D. mawsoni* fishery is clearly on the side of risks. Because the risks will only increase as climate change proceeds, a strong case can be made for completely excluding fishing from a large fraction of the Ross Sea shelf and slope ecosystem. At the very least, the possibility of a toothfish population collapse and/or other ecosystem impacts should be weighed against the economic benefits to the relatively small number of participants in the fishery. Current fishery regulations are only precautionary in the sense that they could have been worse. However, given the poorly justified and relatively high current harvest of Antarctic toothfish, a precautionary approach now would scale back or eliminate fishing until there is a better understanding of its likely consequences, both for the toothfish and its ecosystem.

Nearly a decade ago, Robert May published an article entitled 'The use and abuse of mathematics in biology' (May 2004). He stated that 'Perhaps most common among abuses, and not always easy to recognize, are situations where mathematical models are constructed with an excruciating abundance of detail in some aspects, whilst other important facets of the problem are misty or a vital parameter is uncertain to within, at best, an order of magnitude. It makes no sense to convey a beguiling sense of 'reality' with irrelevant detail, when other equally important factors can only be guessed at.' Those who feel that they can predict the impact of a substantial continuing catch of Antarctic toothfish on the basis of what is now known about that species and its ecological relationships are likely to either be guilty of such abuse or of accepting the word of other abusers.

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