The Scotia Sea krill fishery and its possible impacts on dependent predators: modeling localized depletion of prey
Author(s): Éva E. Plagányi and Doug S. Butterworth
Source: *Ecological Applications*, Vol. 22, No. 3 (April 2012), pp. 748-761
Published by: Wiley
Stable URL: http://www.jstor.org/stable/23213914
Accessed: 09-03-2016 13:07 UTC

Ecological Applications, 22(3), 2012, pp. 748–761

The Scotia Sea krill fishery and its possible impacts on dependent predators: modeling localized depletion of prey

Éva E. Plagányi[1] and Doug S. Butterworth

Marine Resource Assessment and Management, Department of Mathematics and Applied Mathematics, University of Cape Town, Private Bag, Rondebosch 7701 South Africa

Abstract. The nature and impact of fishing on predators that share a fished resource is an important consideration in ecosystem-based fisheries management. Krill (*Euphausia superba*) is a keystone species in the Antarctic, serving as a fundamental forage source for predators and simultaneously being subject to fishing. We developed a spatial multispecies operating model (SMOM) of krill–predator fishery dynamics to help advise on allocation of the total krill catch among 15 small-scale management units (SSMUs) in the Scotia Sea, with a goal to reduce the potential impact of fishing on krill predators. The operating model describes the underlying population dynamics and is used in simulations to compare different management options for adjusting fishing activities (e.g., a different spatial distribution of catches). The numerous uncertainties regarding the choice of parameter values pose a major impediment to constructing reliable ecosystem models. The pragmatic solution proposed here involves the use of operating models that are composed of alternative combinations of parameters that essentially try to bound the uncertainty in, for example, the choice of survival rate estimates as well as the functional relationships between predators and prey. Despite the large uncertainties, it is possible to discriminate the ecosystem impacts of different spatial fishing allocations. The spatial structure of the model is fundamental to addressing concerns of localized depletion of prey in the vicinity of land-based predator breeding colonies. Results of the model have been considered in recent management deliberations for spatial allocations of krill catches in the Scotia Sea and their associated impacts on dependent predator species.

Key words: Antarctic; ecosystem model; krill; localized depletion; multispecies model; operating model; predator–prey; uncertainty.

Introduction

Mathematical models have a long history of use to advance and complement ecological thinking. Many early models were largely theoretical, given difficulties in estimating the values of model parameters, particularly for the more complex multispecies and ecosystem models. The past two decades have seen an increased need expressed for quantitative approaches to evaluate the nature and impact of fishing on predators that share a fished resource (e.g., Plagányi and Butterworth 2005, Hill et al. 2006). Examples include the potential impact of the South African pelagic fishery on African penguins *Spheniscus demersus* (e.g., Pichegru et al. 2010, Butterworth et al. 2011), impacts of the Californian fishery for rockfish on seabird productivity (Field et al. 2010), as well as examination of spatially explicit management decisions pertaining to the endangered Steller's sea lion *Eumetopias jubatus* in the North Pacific (Wolf and Mangel 2008, Lander et al. 2009), and krill-dependent predators in the southern hemisphere (Alonzo et al. 2003, Constable 2006*a*, Hill et al. 2006, 2009). It is increasingly acknowledged that forage species such as krill (*Euphausia superba*) play a keystone role as prey for a variety of higher-trophic-level species (Reid and Croxall 2001). Poorly regulated fishing potentially threatens the future survival of not only the forage species themselves, but also the predators dependent on them. Mathematical models are useful to quantify species interactions, environmental and fishing impacts, and to assess and compare the ecosystem risks of alternative fishing strategies.

One pragmatic way forward involves constructing a minimally realistic model (MRM; sensu Punt and Butterworth 1995), which restricts focus to important processes and interactions only. Such models are intermediate in complexity in terms of bridging the gap between single-species assessment models and more complex ecosystem models that encompass many more species groups or model compartments (Plagányi 2007). They nevertheless include enough complexity to allow sensitivity analysis of critical model components, such as the functional relationships between predators and prey density (Plagányi 2007).

This paper summarizes a spatial multispecies operating model (SMOM) of krill–predator–fishery dynamics

Manuscript received 7 March 2011; revised 25 July 2011; accepted 27 September 2011. Corresponding Editor: S. S. Heppell.

---

[1] Present address: Marine and Atmospheric Research CSIRO, P.O. Box 2583, Brisbane 4001 Australia. E-mail: Eva.Plaganyi-Lloyd@csiro.au

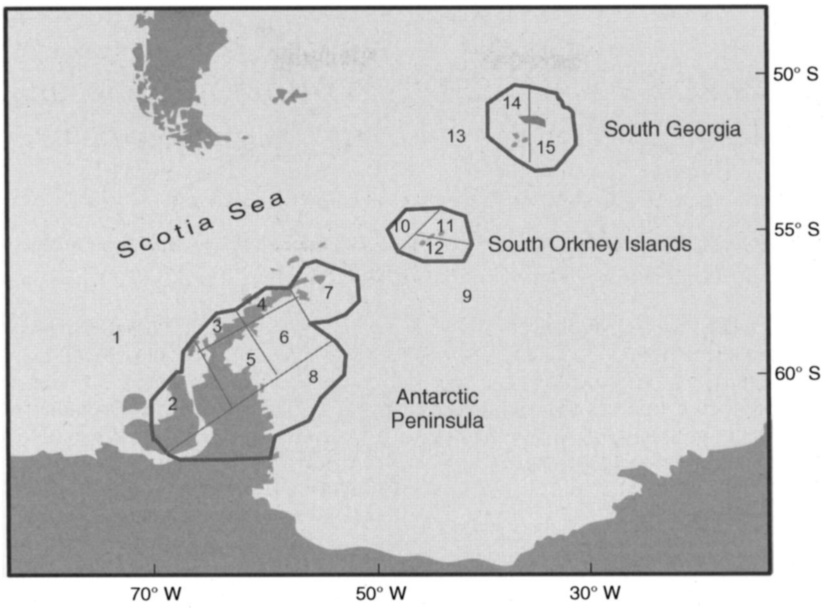

FIG. 1. Map (after Hewitt et al. 2004) showing the Scotia Sea region and subdivision into 15 small-scale management units (SSMUs). SSMUs are (1) Antarctic Peninsula Pelagic Area (APPA), (2) Antarctic Peninsula West (APW), (3) Drake Passage West (APDPW), (4) Drake Passage East (APDPE), (5) Bransfield Strait West (APBSW), (6) Bransfield Strait East (APBSE), (7) Elephant Island (APEI), (8) Antarctic Peninsula East (APE), (9) South Orkney Pelagic Area (SOPA), (10) South Orkney West SOW), (11) South Orkney North East (SONE), (12) South Orkney South East (SOSE), (13) South Georgia Pelagic Area (SGPA), (14) South Georgia West (SGW), and (15) South Georgia East (SGE).

in the Scotia Sea that has been used to take into account some of the major sources of uncertainty in a multispecies model with applications to management. Operating models (OMs) are mathematical-statistical models, such as MRMs, that represent "true" underlying resource dynamics, as a basis for simulation trials to evaluate the trade-offs associated with alternative management options (Rademeyer et al. 2007). OMs (especially single-species models and MRMs) are typically "conditioned" on available information (including fisheries and ecological data, analogous to fitting an assessment model), by adjusting parameter values to ensure plausibility and consistency with this information (Rademeyer et al. 2007).

SMOM has been developed in response to requests for scientific advice by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). CCAMLR was one of the first bodies to explicitly account for the requirements of natural predators of the species being fished, by setting a target level for krill at 75% of the median pre-exploitation biomass (SC-CAMLR 1990, Butterworth et al. 1994). Although this measure is very conservative by most fisheries management standards, krill catches could nonetheless make an appreciable ecosystem impact if they are concentrated in small localized areas that simultaneously serve as important foraging grounds for dependent predators. Both SMOM and two other approaches, EPOC (ecosystem productivity ocean climate; Constable 2006*b*) and Foosa (Watters et al. 2005, 2006, 2008, CCAMLR 2008), have been used to inform advice concerning subdivision of the total catch for krill among 15 small-scale management units (SSMUs) in the Scotia Sea and Drake Passage (CCAMLR statistical subareas 48.1–48.3; Fig. 1). This is sometimes also referred to as the Antarctic Peninsula region, but for simplicity we hereafter refer simply to the Scotia Sea region.

The primary aim of this research is to assess and to ameliorate current and future potential impacts of fishing on predators, given that localized depletion effects may already be occurring and that krill catches may increase substantially in the future. To this end, we use SMOM to compare four catch allocation options for distributing the catch limit among the SSMUs in the Scotia Sea, as put forward by Hewitt et al. (2004): proportional to (1) historical catch within the SSMU; (2) estimated predator demand in the SSMU; (3) estimated standing stock of krill in the SSMU; and (4) standing stock less annual predator demand in the SSMU.

METHODS

General modeling approach

Ecosystem models, especially larger whole-ecosystem models, are typically not conditioned (fitted) to data (Plagányi 2007, Rose et al. 2010). In the case of the Scotia Sea, there are insufficient data to construct a fully conditioned model. The approach adopted was thus to utilize data wherever possible and to integrate results across key uncertainties. This was achieved by using a number of alternative models, the so-called reference set (Rademeyer et al. 2007) of models (rather than a single

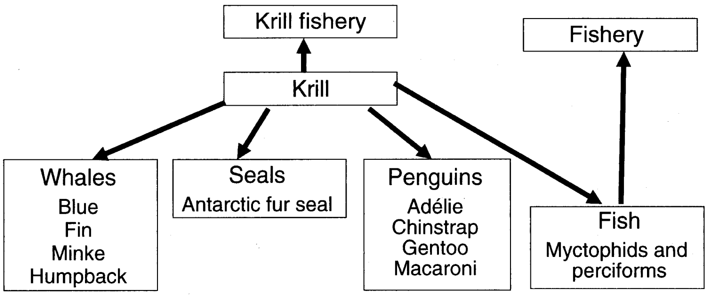

FIG. 2. Schematic summary of interactions included in the spatial multispecies operating model (SMOM). The relative abundances of each of the four generic predators vary among the SSMUs. Krill is the only prey species.

model), that collectively capture some of the key model parameterization uncertainties. This paper refers also to Foosa (Watters et al. 2008), as SMOM and Foosa were used in conjunction for a better coverage of the uncertainties. Moreover, the responsible CCAMLR Scientific Working Group on Statistics, Assessments and Modelling (WG-SAM or SAM) compiled a set of reference observations for validating and conditioning proposed models. These observations were largely qualitative and expressed in relative rather than absolute terms (e.g., abundances expressed as indices rather than numbers), and were translated into numerical terms (the numerical calendar; Hill et al. 2008) by WG-SAM (see Appendix D: Tables D1–D5). SMOM was conditioned using this set of reference observations for the Scotia Sea (hereafter referred to as the "SAM calendar"). In combination with simulations that integrate across a broad range of uncertainty, this approach serves as a contribution to efforts to distinguish among the merits of alternative spatial subdivisions of the krill catch in the Scotia Sea.

Model structure

The operating model (OM) developed to simulate the dynamics of the Scotia Sea ecosystem includes all 15 SSMUs (Fig. 1) and uses a six-month (two season) time-step to update the numbers of krill in each of the SSMUs, as well as the numbers of predator groups in each of these areas. The model currently includes four "generic" predator groups (penguins, seals, fish, and whales) and a single prey group in the form of krill (Fig. 2).

The OM is coded in AD Model Builder (Fournier et al. 2011). Krill dynamics are governed by a modified discrete logistic model, whereas the predator groups' dynamics are represented using delay difference equations (Tables 1–2; see Appendix A for a full description). The relative fishing effort per SSMU is computed by spatially distributing the total krill catch using one of the four catch allocation options (Table 3). There are no appropriate predator time series data available at the

TABLE 1. Summary of key model equations, including discrete prey equation and the delay difference equation applied to the three predator groups (penguins, seals, fish) for each of the summer and winter seasons.

Description	Equation
Krill	$B^a_{t+1} = B^a_t + r^a_t B^a_t\left[1 - \left(\frac{B^a_t}{\mathrm{K}_a}\right)\right] - \frac{1}{\omega_j}\sum_j \frac{\lambda^j B^a_t N^{j,a}_{y,\mathrm{seas}}}{B^a_j + B^a_t} - F^a_t B^a_t$
Predators (penguins, seals, fish) (summer)	$N^{j,a}_{y+1} = N^{j,a}_y\sqrt{(S^j_{s1})(S^j_{s2})} + (N^{j,a}_{y-T+1})q^j f(B^a_{y-T+1})^j P^j S^{*,j}_{\mathrm{juv}}\left(1 - \frac{N^{j,a}_y}{K^{*,j,a}}\right)\left((S^j_{s1})(S^j_{s2})\right)^{(T-1)/2}$
Predators (winter)	$N^{j,a}_{y,s2} = N^{j,a}_y(\sqrt{S^j_{s1}}) + (N^{j,a}_{y-T+1})q^j f(B^a_{y-T+1})^j P^j S^{*,j}_{\mathrm{juv}}\left(1 - \frac{N^{j,a}_y}{K^{*,j,a}}\right)(S^j_{s1})^{(T-1)/2}(S^j_{s2})^{(T-2)/2}$
Breeding success as a function of krill biomass	$f(B^a_y)^j = \frac{\alpha^{j,a}\frac{B^a_y}{K_a}}{(\alpha^{j,a} - 1) + \frac{B^a_y}{K_a}} e^{(\varsigma_{ay} - \sigma^2_{BR}/2)}$
Steepness of predator–prey interaction relationship	$h^j = \frac{\alpha^{j,a}}{5\alpha^{j,a} - 4}$

Notes: The steepness parameter h^j (taken to be the same for all SSMUs *a*) largely controls the shape of the relationship between predator breeding success and prey availability. See Table 2 for a list of symbols and Appendix A for a full description of the model. Note that $N_y = N_{y,s1}$.

Table 2. List of the model variables and parameters, which appear in Table 1 and Appendix A, together with descriptions and values.

Variable/parameter	Description	Value [source]
B_y^a	biomass of krill in small-scale management unit (SSMU) a at time step t (with two time steps per year y)	
$N_y^{j,a}$	number of predator species j in SSMU a in year y	
$N_{y,\mathrm{seas}}^{j,a}$, $N_{y,\mathrm{s1}}^{j,a}$, $N_{y,\mathrm{s2}}^{j,a}$	number of predator species j in SSMU a at the start of seasons (seas) s1 (summer) and s2 (winter) in year y	
F_t^a	fishing proportion (catch $= F_t^a B_t^a$) on krill in SSMU a at time step t	see Table 3
$f(B_y^a)^j$	breeding success factor (multiplier for P), which is a nonlinear function of the biomass of krill in SSMU a in year y for predator species j	see Fig. 3
r_t^a	intrinsic growth rate of krill in SSMU a at time t (seasonal dependence not indicted by a subscript to avoid cluttering the notation throughout)	r_t^a (summer) $= 0.3$; r_t^a (winter) $= 0.4$; except South Georgia ($a = 13–15$) $r_t^a = 0.75 r_t^a$ [1]
K_a	average carrying capacity of krill in SSMU a	computed (Appendix A: Eq. A.12)
λ^j	maximum per capita consumption rate of krill by predator species j	from associated computations [2]
B_j^a	krill biomass when the consumption and hence also birth rate of species j in SSMU a drops to half of its maximum level	computed (Appendix A: Eq. A.10)
ω_j	proportion of mature females in the mature population of predator species j	0.5 (penguins); 0.67 (seals); 0.5 (fish); 0.5 (whales) [2]
T	age at first maturity, taken for simplicity to be one less than the age at first reproduction (i.e., assuming a one-year gestation or development period)	3 (penguins); 4 (seals); 3 (fish); 5 (whales) [2]
q^j	fraction of chicks/pups that are female for predator species j	0.5
P^j	maximum proportion of fledged chicks or pups surviving to the end of their first year of life per pair of predator j per year	0.91 (penguins) [3]; 0.88 (seals) [4]; 3.0 (fish); 0.5 (whales) [5]
$K^{*,j,a}$	carrying-capacity-related term for predator species j in SSMU a	computed using R^j (Appendix A: Eq. A.14); whales initial $N/K = 0.1$
S_{seas}^j	post-first-year annual survival rate of predator species j in season seas	Table 4
$S_{\mathrm{juv}}^{*,j}$	maximum first year (juvenile) survival rate (post-fledging or post-weaning) of predator species j	Table 4
h^j	"steepness" parameter for the breeding success function for each predator species j	Table 4
α^a, β^a	parameters for the (predator-dependent) breeding success function for SSMU a, with $\beta = (\alpha - 1)K_a$	computed using $K^{*,j,a}$ and h^j (Appendix A: Eqs. A.9 and A.10)
ζ_{ay}	parameter that reflects fluctuation about the expected curve for SSMU a in year y, which is assumed to be normally distributed	estimated
σ_{BR}	standard deviation of normal distribution describing fluctuation about the breeding success curve	varied from 0.01 to 0.25
R, R^j	recent annual steady growth rate of krill and predator species j	0.0 except whales (0.06) (CCAMLR WG-EMM)†

Note: All rate-related parameters have units yr^{-1}.

Sources: 1, Mori and Butterworth (2006); 2, Hill et al. (2007); 3, Crawford et al. (2006); 4, Boyd et al. (1995); 5, Taylor et al. (2007).

† Commission for the Conservation of Antarctic Marine Living Resources Working Group on Ecosystem Monitoring and Management.

correct scale to which to formally fit the model. However, models contributing to management advice on this issue need to demonstrate that they are consistent with a compiled list of likely changes in predator and krill abundances in the Scotia Sea (termed the SAM calendar; Hill et al. 2008). The SAM calendar consists of spatially resolved values for the density of krill, and the abundance of "generic" seals, penguins, and whales in three years (see Appendix D: Tables D1–D5). The calendar broadly depicts historic changes in biomass; for example, a higher krill density over the period from 1970 to 1985 than over the more recent period from 1986 to 2007. The trends for predator species were assumed the same in SSMUs 1–12 and in 13–15, but their numbers were scaled using SSMU-specific estimates of abundance (Hill et al. 2008).

TABLE 3. The annual krill catch per SSMU, together with the fishing proportions corresponding to each of catch allocation options 1–4.

SSMU	Area name	Catch (Gg)	Opt 1	Opt 2	Opt 3	Opt 4
1	Antarctic Peninsula Pelagic Area	25.4	0.03	0.18	0.15	0.05
2	Antarctic Peninsula West	7.4	0.01	0.04	0.03	0.02
3	Drake Passage West	228.0	0.23	0.01	0.01	0.01
4	Drake Passage East	103.0	0.11	0.02	0.01	0.01
5	Bransfield Strait West	11.5	0.01	0.02	0.02	0.02
6	Bransfield Strait East	6.0	0.01	0.02	0.02	0.01
7	Elephant Island	94.9	0.10	0.02	0.02	0.02
8	Antarctic Peninsula East	0.03	0.00	0.08	0.06	0.02
9	South Orkney Pelagic Area	6.3	0.01	0.22	0.22	0.18
10	South Orkney West	217.0	0.22	0.01	0.06	0.09
11	South Orkney North East	15.9	0.02	0.01	0.01	0.03
12	South Orkney South East	19.5	0.02	0.03	0.02	0.06
13	South Georgia Pelagic Area	7.8	0.01	0.22	0.28	0.40
14	South Georgia West	31.4	0.03	0.09	0.06	0.05
15	South Georgia East	209.0	0.21	0.03	0.03	0.03

There are a number of ways in which predator dynamics could be linked to the abundance of krill. In the interest of constructing as simple a model as possible, consistent with the MRM philosophy, this is not effected through a term related to consumption. Rather, the models developed assume that breeding success is likely to be the most sensitive of the various demographic parameters to changes in prey abundance (Boyd et al. 1995, Croxall et al. 1999). Density dependence in predators such as seals and penguins is assumed to affect primarily the youngest age classes (e.g., Doidge et al. 1984, Boyd et al. 1995, Stokes and Boersma 2000). A breeding success factor $f(B_y^a)$ (see Table 1 and Appendix A: Eq. A.2) is thus formulated as a function of the available biomass of krill (i.e., krill biomass in SSMU a in year y) and acts as a multiplier of the juvenile recruitment parameters, namely the reproductive rate P and/or the juvenile survival rate. Thus the predator–prey interaction term links predator breeding success directly (and nonlinearly) with prey abundance, avoiding the need for an explicit consumption-related term.

A single parameter value h (see Table 1 and Appendix A: Eq. A.9) determines the breeding success for each area for predator species j as a function of the average krill unfished biomass in that area (Fig. 3). The parameter h controls the "steepness" of the curve (Francis 1993), and hence the level of krill abundance (relative to the unfished biomass) below which there is an appreciable negative impact on predator breeding success. This level is not well known for most krill-dependent predators, but nevertheless two values of h can be selected that roughly bound the likely range in this relationship (see Fig. 3). Moreover, rather than assuming a deterministic relationship, variability is added whose extent is controlled by the choice of a value for the parameter σ_{BR}, the standard deviation describing the extent of fluctuation about the breeding success curve (see Eq. A.8 in Appendix A).

Accounting for seasonality.—A seasonal component is necessary to temporally separate the fishery from predator demands, particularly for the South Georgia SSMU, which is characterized by a fishery that operates during the winter months. In SMOM, years are split into a "summer" s1 season and "winter" s2 season. The krill population in each SSMU is thus updated each year using two time-steps, with the possibility of setting different growth rates, and catches/fishing proportions for each of the six-month periods s1 and s2 (Appendix A: Eq. A.1). Moreover, whereas consumption estimates for s1 are computed based on the numbers of predators present in each SSMU (and assumed confined to that SSMU because of their breeding), during s2 the predators are assumed to range widely (CCAMLR 2006) and to distribute themselves in the same proportions as the relative abundance of krill per SSMU at the end of s1 (Appendix A: Eq. A.5).

Krill fishery.—The model assumes that the krill fishery does not operate in an SSMU once krill density falls

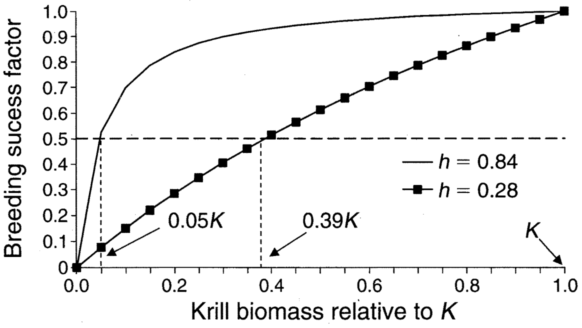

FIG. 3. Plot of the relationship modeled between predator breeding success and krill abundance relative to the average krill carrying capacity level, K, in each SSMU. The shape of the curve is determined by the steepness parameter, h (see Appendix A: Eq. A.9), with illustrative values for penguins (0.28) and seals (0.84) used in the plot. The illustrative curves show examples of a near-linear decrease in breeding success as krill abundance decreases (square symbols) and a scenario in which predator breeding success is negatively impacted at relatively low levels of krill abundance only (line only). Thus in the former case breeding success drops to half its maximum level when krill biomass is 39% of K compared with a much lower 5% of K in the latter case.

below a threshold value, preliminarily set (arbitrarily) at 20% of the level at the start of the projection period. Thus in some cases the krill catch may be less than the spatial catch allocation. This provides a rough way of accommodating an economic concern of the fishery regarding threshold krill densities below which fishing becomes uneconomical (Hill et al. 2009). It parallels the notion from optimal foraging theory in which predators move on when prey density falls below a threshold level.

A reference set of OMs to bound uncertainty.—The initial reference set of OMs used comprises 12 alternative combinations per predator to broadly bound the uncertainty in the choice of survival rate estimates as well as in the breeding success relationship. Sensitivity analyses showed that survival rates are the parameters to which the model results are most sensitive, but little information exists to estimate them reliably.

For each predator species, the following parameter values are thus input: (1) a high, medium, and low adult annual survival rate; (2) an upper and lower bound for the maximum juvenile annual survival rate; and (3) two alternative values (h_1, h_2) to roughly bound the likely "steepness" of the breeding success relationship (Fig. 3).

This leads to a total of $3 \times 2 \times 2 = 12$ alternative OMs to represent the dynamics of each predator. This number of combinations then could be raised to a power equal to the number of predators included, so that the number of OMs would become extremely large. Given computational constraints, coupled low, medium, and high survival rate scenarios for each predator are assumed to restrict the number of operating models to 12. A total of 10 replicates of each OM are run, yielding a total of 120 simulations per scenario.

Model parameter values.—To facilitate model comparisons, SMOM and Foosa used the same model inputs wherever possible (CCAMLR 2006, 2008). Most of these inputs, including essential information on the total demand for krill from key predator species in each SSMU, are summarized in Hill et al. (2007). Parameters for several species were combined by Hill et al. (2007) to represent "generic" predators as this was considered the most pragmatic way to proceed, notwithstanding that differences among individual species may be important.

Krill

Colder, more southerly, water is more optimal for krill growth, given that growth declines for temperatures >1°C (Atkinson et al. 2006). The basic krill intrinsic growth rate parameter is set at 0.3 (summer) and 0.4 (winter; Table 2; see also Mori and Butterworth 2006). The predator consumption rate parameters λ^j are based on the estimates presented in Hewitt et al. (2004). Krill numbers are converted to biomass assuming an average krill mass of 0.46 g (Hill et al. 2007). The relative spread of fishing effort across the different SSMUs under each of the four catch allocation options is as shown in Table 3.

There are no empirical data at the correct scale to inform on modeling of krill movement. The model version presented here assumes no movement of krill between SSMUs. Although it is possible to include movement, this serves as a lower conservative bound because it explores a scenario in which locally depleted prey is not easily replenished by transport processes. In contrast, Foosa included a high movement scenario. The different model structures representing the same ecosystem are useful in sharing the focus on different aspects of model structural uncertainty.

Predators

The same delay difference equation is used to describe "mature" females (i.e., adult females past the age-at-first-parturition or first laying) of all predators (penguins, seals, fish) except whales. Given the large movements undertaken by whales, their dynamics are not determined at the individual SSMU scale but rather based on the total prey abundance across all the SSMUs. Moreover, all whales are assumed to have migrated out of the area as it is modeled during winter. No whale catches are included given their low impacts over the relatively recent period considered. The other predators in the Scotia Sea region are not confined to their SSMUs during the winter months (CCAMLR 2006). In the model, they are assumed to distribute themselves according to the relative abundance of krill in the region, and then to return again to their natal SSMUs at the start of spring. An important assumption in SMOM is that the fishery acts as an "inferior" competitor to predators (fishing occurs only after consumption by predators is modeled to have taken place).

Given estimates of the predator growth rates R^j from Hill et al. (2008), the only parameter not yet accorded a value in the equilibrium equation (Appendix A: Eq. A.13) is the maximum predator breeding success parameter P^j. Note that the actual realized breeding success is adjusted by the value of $f(B_y^a)$, which is a function of the krill depletion level relative to average carrying capacity K (see Fig. 3). The average number of offspring per mature female that survive the first year of life is given by the product $f(B_y^a)P^jS_{\mathrm{juv}}^j$, which includes both intra- and interspecific density-dependent components. In combination, these terms thus roughly capture the pregnancy rate, survival until fledging (for penguins) or until pups leave their natal colony (for seals), and survival of juveniles to the end of the first year of life. This method, elaborated in Appendix A, provides a means for accounting for density dependence when the exact underlying mechanisms are not known or cannot be differentiated.

Method for conditioning model: historic runs

A number of approaches were used to condition the model to the SAM calendar to roughly represent historic changes in predator and krill abundances in the Scotia Sea over the period 1970–2006. First, Leslie matrix analysis (Appendix B) was used to explore combinations of survival rate estimates (and other demographic parameters) capable of reproducing the observed population growth rates as

TABLE 4. Summary of choices of alternative combinations of S and S_{juv} for each predator group, estimated by fixing other demographic parameters (see Appendix B).

Predator group j	Adult annual survival rate S^j	Juvenile annual survival rate $S^{*,j}_{\mathrm{juv}}$	Steepness of predator–prey interaction term h^j
Penguins	0.90	0.95	0.28
	0.89	*0.935*	*0.25*
	0.88	0.92	0.23
Seals	0.96	0.93	0.84
	0.94	*0.91*	*0.79*
	0.92	0.89	0.74
Whales	0.98	0.91	0.99
	0.975	*0.85*	*0.98*
	0.97	0.80	0.97
Fish	0.72	0.65	0.50
	0.71	*0.65*	*0.40*
	0.70	0.65	0.30

Notes: The values in italic type are computed as the average of the upper adult survival rate and lower juvenile survival rate parameter values. The steepness h^j parameters are derived by fitting to the observed historic trends (see Appendix A). The reference set comprised 12 combinations of these parameters.

summarized in the SAM calendar. Secondly, the model was conditioned (see Appendix A for likelihood formulations) to the SAM-calendar reference observations to assist in refining parameter estimates for each of penguins, seals, and whales. The main method of conditioning involved estimating the shape parameter (the "steepness," h^j) of the predator–prey interaction formulation. This proved particularly useful for informing two aspects of the model:

1) For fish, there are no calendar observations describing the change in the relative abundance over time, but an estimate of the recent abundance per SSMU is provided in Hewitt et al. (2004). Moreover, historic catch data were sourced (Appendix C: Table C1). The OM was thus used to estimate the 1970 starting abundance of fish in each SSMU that would result in the recent abundance given the historic catch record and dynamics as described in Appendix A: Eq. A.2.
2) For each of the three predator groups penguins, seals, and whales, the parameter h^j that resulted in the best fit to the SAM calendar numerical values was estimated for each combination of survival values.

OM estimates of h^j for each predator are shown in Table 4, with slightly different values of h estimated for different combinations of adult and juvenile survival rate values. Note that following application of the density-dependent term (Appendix A: Eq. A.8), the "realized" survival rate values (Appendix C: Table C2) are much less than the maximum possible juvenile survival rate parameter values that are input. The model could be further refined by allowing different h^j values for different SSMUs (or groupings of SSMUs), but the approach adopted here has been to start as simple as possible, so that it seemed appropriate to assume a common h^j for each predator group.

Forward projections to inform management

The conditioned model is used to provide 120 realizations of projections over the 40-year period 2007–2046. Krill catches are assumed to continue at a constant level for the first 20 years, and thereafter are set to zero to assess the extent of resource recovery, given that a key principle included in CCAMLR's Article II Convention identifies the need to minimize the risk of changes that are not potentially reversible over two or three decades. Resource recovery is thus considered an important performance statistic in comparing the performance of alternative spatial krill subdivisions.

The relative risks of depleting predator populations below 75% of their level in the unfished scenario under the different catch allocation options are assessed across a range of increasing krill catch levels, which are specified by applying a so-called yield multiplier that scales the catch relative to the current precautionary catch limit. In CCAMLR's krill assessment, krill yield is calculated as a proportion (γ) of the pre-exploitation biomass. Krill and predator abundance at the end of the projected 20-year fishing period are compared with equivalent no-fishing trials to compute the probability of being less than 75% of the median no-fishing level. It is important to assess impacts relative to comparable no-fishing trials to avoid drawing erroneous conclusions based on population trends. For example, decreasing population trends may be the result of model initialization or environmental factors. Risk probabilities are reported as averages, assuming equal weighting across the reference set of 12 alternative sets of parameter values for the model that yields 12 OMs.

RESULTS

The conditioned trajectories of penguin, seal, and fish abundance (expressed as abundance [number of individuals]) for three illustrative SSMUs and krill biomass are shown in Fig. 4. The plots show comparisons with the empirical abundance estimates (SAM calendar) from Hill et al. (2008). For krill and fish, the historic catches are also shown.

As a preliminary illustration of differences resulting from alternative allocations of the krill catch limit among the SSMUs, Fig. 5 compares the median penguin abundances as projected under each of the four catch allocation options and in all SSMUs with penguins present. The penguin trajectories are selected to be shown here because of their greater sensitivity to changes in krill availability.

In the interests of brevity, detailed results are illustrated for a single SSMU only, SSMU 3 (Drake Passage West; Fig. 6), when compared across the four different catch allocation options. Results were broadly consistent across all SSMUs (see Plagányi and Butterworth [2007, 2008] for further results). For presentation purposes, trajectories of predator group abundances are summarized by showing annual median values and 90% probability envelopes (Fig. 6). These shade plots give a truer reflection of the

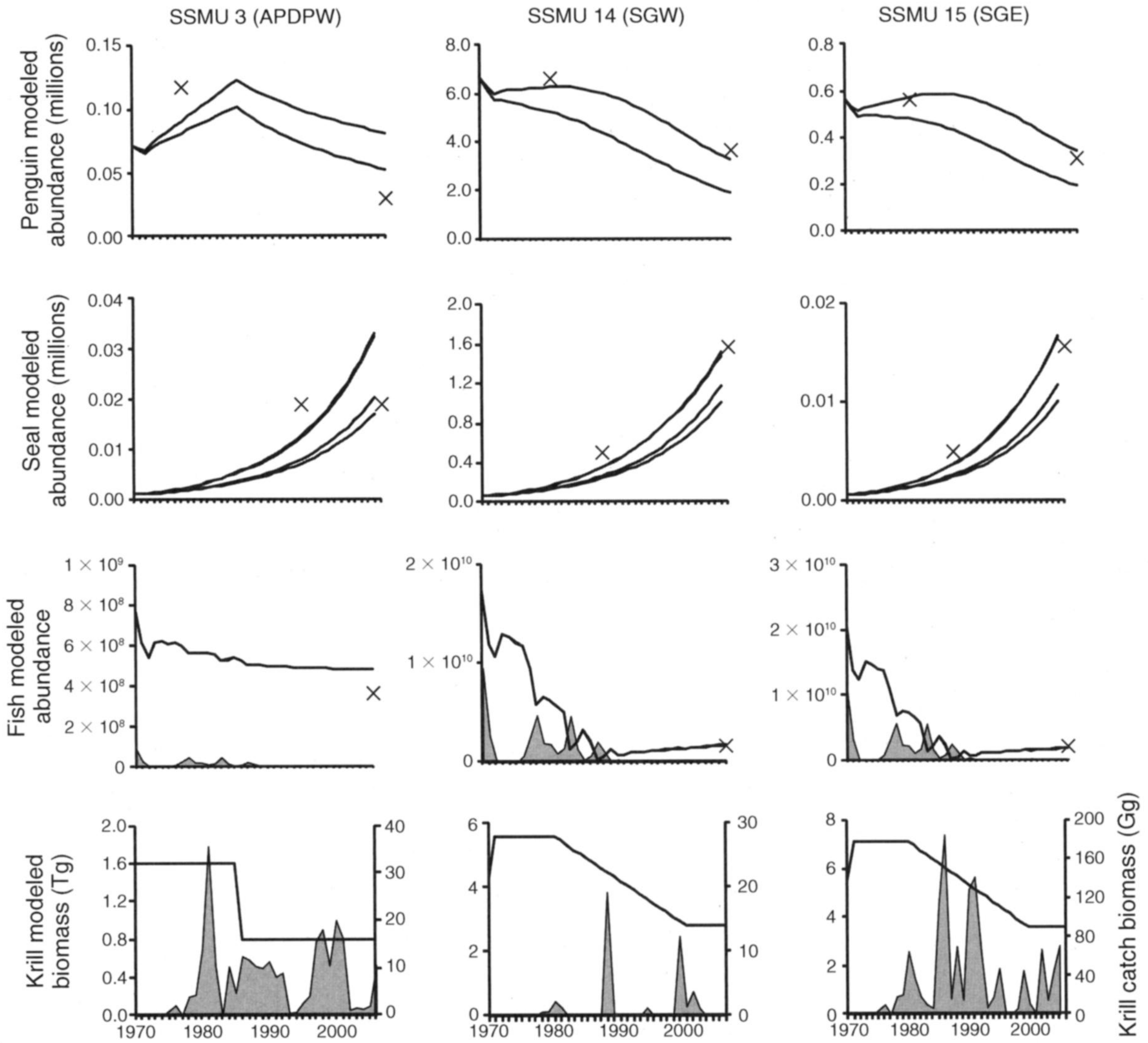

FIG. 4. Conditioned trajectories of penguin, seal, and fish abundance (expressed as millions), for the period 1970–2006, in three illustrative SSMUs from 12 operating models (OMs) that constitute the reference set, and when using the SAM calendar krill biomass as an input (bottom row; see *Methods: General modeling approach* for an explanation of the SAM calendar). The crosses represent empirical abundance estimates from Hill et al. (2008). For krill and fish, the historic catches are shown as the shaded regions in the plot. As the krill catches were very small compared to krill biomass, these are plotted on a different scale (thousands of tons), which is shown on the right-hand vertical axis for easier viewing. Whale abundance (not shown) summed over all SSMUs increased approximately exponentially and fitted the empirical estimates closely.

uncertainty inherent in multispecies models than plots presenting results in point estimate form only. The projected whale numbers across all SSMUs are not presented here as they hardly differed across the scenarios.

Simulations to compare the four catch allocation options demonstrated that, overall, option 1 resulted in relatively poorer performance (Figs. 5 and 6). This option, which is based on historic catches, leads to some two-thirds of the krill catch being taken from three non-pelagic SSMUs (3, 10, and 15; Table 3); hence it is not surprising that this option performs poorly in terms of predator trends in these regions (Figs. 5 and 6). A large initial decrease in penguins is also evident in SSMU 7, which has the next largest historic catch (Fig. 5). Catch allocation options 2, 3, and 4 to a lesser extent, result in the majority of the krill harvest (see Table 3) being taken from the three pelagic areas (SSMUs 1, 9, and 13) because these had the highest observed krill standing stocks during the CCAMLR_2000 survey (Hewitt et al. 2002, 2004). Penguins and seals are confined to the non-pelagic areas during the breeding season, but whales and fish are present in all areas. Penguins thus do better in general under options 2 and 3 because catches are concentrated away from their breeding sites. The exception is SSMU 14 under option 2, for which the harvest from this region is relatively large (Table 3, Fig. 5). Catch allocation option 4 performs

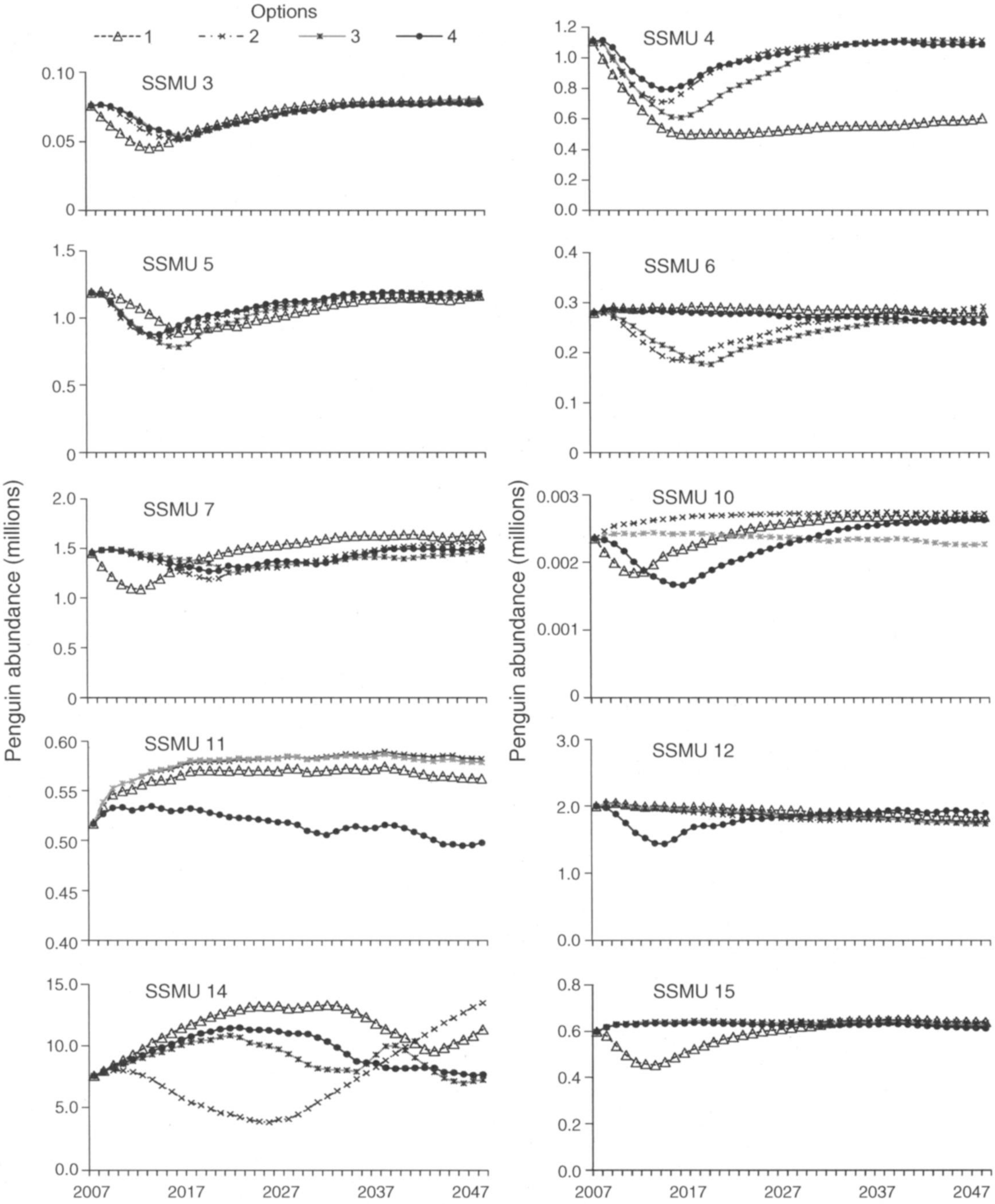

FIG. 5. Comparison of median penguin abundance projections (in millions) in SSMUs with penguins present and under catch allocation options 1–4. Medians are from 120 model realizations.

poorly in the South Georgia and South Orkney areas (SSMUs 11–15; Fig. 5), which have the largest abundances of penguins and seals.

These results are consistent with previous work (Watters et al. 2008) that suggested catch allocation options 1 (based on historical catch) and 4 (proportional to estimated standing stock less predator demand per SSMU) performed worse than options 2 and 3, and that those last two options were the most difficult to distinguish in terms of performance. Attention was thus focused on some of the possible tradeoffs in selecting between catch allocation option 2 (allocation proportional to the estimated predator demand in the SSMU) and 3 (allocation proportional to the estimated standing stock of krill in the SSMU) in terms of catch levels, fishery distributions, and risks to predator populations. The total krill catch allowed (for the resource as a whole) is computed as a proportion (γ) of the

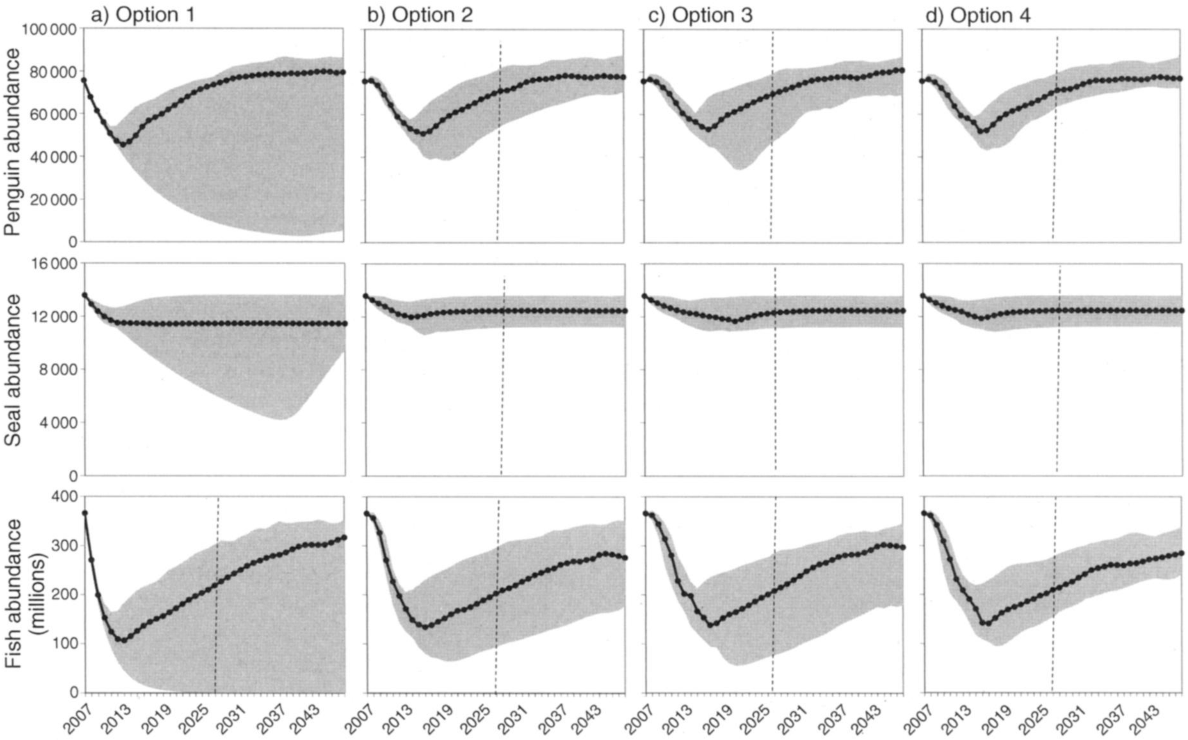

FIG. 6. Future projections generated by SMOM for penguin, seal, and fish abundance in SSMU 3 compared under catch allocation option: (a) option 1 (proportional to historical catch within the SSMU), (b) option 2 (proportional to estimated predator demand), (c) option 3 (proportional to estimated krill standing stock), and (d) option 4 (proportional to standing stock less annual predator demand in the SSMU), from 120 OM projection replicates. Annual median values are shown as a dark dotted line, and the shaded areas show 90% probability envelopes. Note that projections assume fishing occurs for the first 20 years but is set to zero thereafter (indicated by a vertical line) to allow the extent of subsequent resource recovery to be assessed.

unexploited population biomass (B_0) (Butterworth et al. 1994), where γ is currently set at 0.093. The impact on krill populations was assessed by computing the probability that krill abundance measured at the end of the fishing period is less than 75% of the median abundance from comparable no-fishing trials, with a large variation in the responses predicted for the different SSMUs (Fig. 7). The average probability increased approximately linearly as yield multiplier values (i.e., values that multiply γB_0) were increased from 0.15 (equivalent to the current trigger level; the trigger level is less than the total allowable catch, and once catches exceed this level, it becomes mandatory for CCAMLR to implement spatial subdivision of the catches) to 2 (Fig. 7). The model-estimated probabilities that penguin and seal populations would be depleted below 75% of the abundances from comparable no-fishing trials, increase markedly at harvest proportions that exceed 0.5γ for both options 2 and 3 (Fig. 8). Results are similar under both options, and it is difficult to discriminate between them, although there is a slightly higher risk predicted under option 2 (Fig. 8).

DISCUSSION

The spatial multispecies operating model (SMOM) described here has contributed to the provision of scientific advice regarding the subdivision of the total krill catch among 15 small-scale management units (SSMUs) in the Scotia Sea. SMOM is relatively simple and has been constructed to require as few parameters as possible — the alternative sets of parameter values that define the OMs of which the reference set is composed are useful in bounding two key areas of uncertainty: the choice of survival rate estimates and of the predator-prey interaction forms. The approach in representing the latter formulation is flexible and accounts for some of the uncertainty pertaining to predator–prey relationships.

Although unconventional in a fisheries management context, conditioning through the use of qualitative trends based on expert knowledge was proposed by CCAMLR as a practical step forward in ecosystem modeling. The conditioning process was useful in reducing some of the uncertainty associated with key model parameters. For example, lower survival rate estimates could be excluded as these had been shown to be incompatible with observed rates of population increase. Moreover, the conditioning process assisted in resolving some of the uncertainty in the response of predators to krill biomass, with penguins predicted to respond earlier to decreasing levels of krill abundance because of the low steepness value of the functional relationship (Table 4, Fig. 3) estimated for that species.

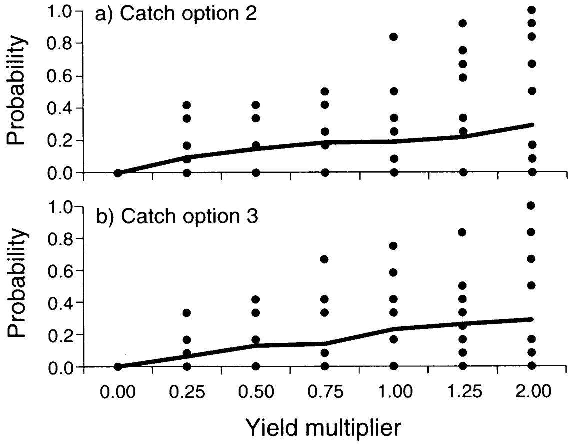

FIG. 7. Probability that krill abundance across all SSMUs, when measured at the end of the fishing period with (a) catch option 2 and (b) catch option 3, is <75% of the abundances from comparable no-fishing trials, with results presented for individual SSMUs (points on plot) and the line indicating the average over all SSMUs. Probabilities are averages, assuming equal weighting, from a reference set including 12 OMs. The catch allocation options are defined in the Fig. 6 caption. The individual SSMUs are not labeled in the figure because the results are broadly representative of the typical responses to be expected rather than exact responses for each individual SSMU. Note that the last yield multiplier value of 2 on the horizontal axis has been added for completeness but, for visualization purposes, is not plotted 0.75 units away from the previous value.

However, the modeling results need to be interpreted fairly broadly given the use of generic predator groups, rather than individual species. Naturally there are individual species differences that may be important, and their behaviors may not be adequately captured by the use of average parameter values for predator groups.

Minimally realistic models (MRMs) are a pragmatic choice in the process of moving from single-species models to the extremely ambitious and demanding aim of a reliable predictive model for all major ecosystem components (Butterworth and Plagányi 2004). The choice of the level of complexity for an ecosystem model is critical, and it is acknowledged that adopting a MRM approach may have consequences on the results due to excluding second order effects. Reducing the number of species considered, or aggregating similar species into groups as in this case, reduces the number of inter-species links that need to be modeled, but consequently also reduces the number of weak links included in the model that may lead to incorrect inferences regarding possible behavior of the system (Yodzis 1998). The approach adopted here adheres to two important guidelines (Fulton et al. 2003) not to aggregate serially linked groups (predator and prey), and similarly not to do so for species, age classes or functional groups with rate constants that differ by more than two- to threefold. Future work could explore the consequences of disaggregating generic species groups into individual species representations.

Fish are major consumers in the system modeled and hence their presence impacts on the other predators. It was therefore considered important to try to represent the fish dynamics as realistically as possible in the model. We accounted for the occasional high fish catches observed in the region; although these analyses could be further refined, they suggest that fish populations in several of the SSMUs are much reduced compared to their starting (1970) levels (Fig. 4). Overall the basic model, as conditioned, successfully reproduces the direction and timing of changes in predator abundances as specified by Hill et al. (2008). Nonetheless, these results should be interpreted broadly as there is currently only weak evidence to support the assumed historic trend in krill biomass.

There is considerable variation among SSMUs in the response to different catch allocation options. However,

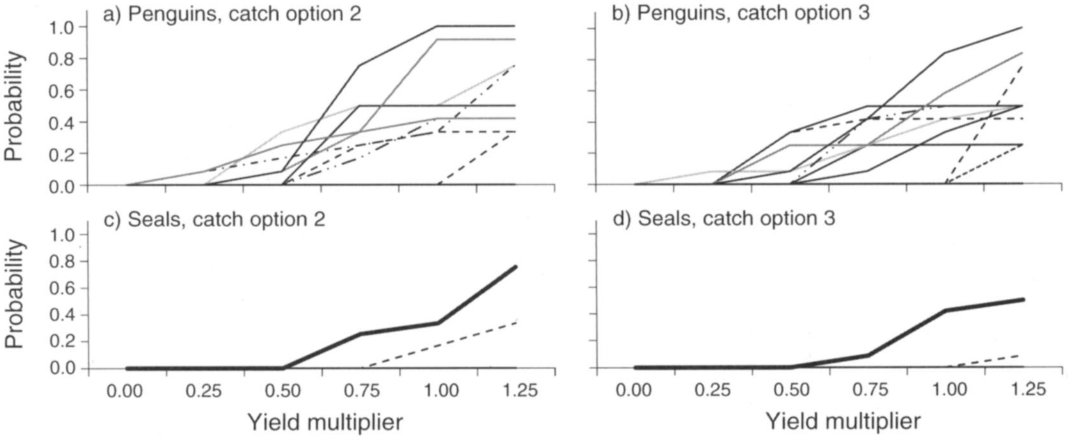

FIG. 8. Model-estimated probability that predator abundance for each SSMU when measured at the end of the fishing period is <75% of the abundances from comparable no-fishing trials, with results presented for individual SSMUs and predator groups. Probabilities are averages by SSMU, assuming equal weighting, over a reference set including 12 OMs. Catch allocation options are defined in the Fig. 6 caption. Note that three of the five seal plots are not distinguishable from the horizontal axis.

although the median projections for predator groups do not always vary substantially, there is an increased risk to predators under option 1 as highlighted by the substantial decrease in the lower probability interval value in some cases (Fig. 6). Whale populations are predicted to continue increasing across all scenarios investigated.

Any assessment of the risk to predators needs to be balanced with an assessment of the risk to the fishery itself. Thus, although option 1 is considered undesirable from a predator perspective, it may be the preferred scenario when considering the costs to and hence the efficiency of the fishery itself. The OMs predict that catches could be greatest in pelagic SSMUs (Table 3). However, although available biomass may be higher in those SSMUs (because the total area of these SSMUs is substantially greater than the area of coastal SSMUs), there is a risk that krill densities in these large pelagic areas could fall below thresholds that are economically viable for the operation of fishing vessels (Hill et al. 2009).

In terms of impacts of increasing krill catches on the krill population, the responses in respect of krill abundance at the end of the fishing period were similar under options 2 and 3 (Fig. 7). There is an increase in risk that krill abundance measured at the end of the fishing period will be less than 75% of the median abundances from comparable no-fishing trials as the harvest proportion increases beyond 0.15γ (the current trigger level). The broad scatter of points in Fig. 7 suggests that, under a no-movement scenario, there is substantial variation in the risk for individual SSMUs that the local krill population abundance falls below 75% of its abundance in comparable no-fishing trials.

The risk that predator populations would be depleted below 75% of the abundances that might occur in the absence of fishing rises markedly at harvest proportions that exceed 0.5γ for both options 2 and 3 (Fig. 8). Results reported here have focused on impacts on penguins and seals rather than fish because of the greater uncertainty associated with the fish trajectories. At moderate harvesting rates, preliminary model results indicated the possibility of high relative impacts on fish when compared to the no-fishing option because fish are assumed to be on a recovery trajectory. Changes in harvest proportions had negligible impacts on whales because of the assumption that whales can move between SSMUs. Despite the considerable uncertainties, some of which at least have been included in SMOM, it was thus possible to discriminate between catch allocation options 1, 4, and 2–3, although less possible to discriminate between options 2 and 3 (see also Watters et al. 2008).

The model and results presented here are part of an ongoing process. The spatial and (ecological) multispecies OM described here is intended for use as part of a management procedure (MP [Butterworth and Punt 1999] or, equivalently, management strategy evaluation, MSE [Smith et al. 1999]). MPs are simulation approaches that test and compare the performance and robustness of a number of alternative management options that are designed to satisfy multiple conflicting objectives. A key aspect of the MP approach is that the method proposed to compute quantitative management advice has been tested across a wide range of scenarios for the underlying dynamics of the resource using computer simulation. An advantage of the process being followed by CCAMLR is that multiple ecosystem models with different model structures and parameterizations are to be used as OM. Ecosystem/multispecies models are difficult to validate and hence if different models give qualitatively similar results, this can increase the confidence in these models. To date, the two approaches SMOM and Foosa have generally predicted qualitatively similar trends in the response of dependent species to alternative krill catch allocation options.

It is recognized that there are a number of key uncertainties and model assumptions that could bias model predictions. Two approaches that have been pursued here in response to this are first to integrate model results across a wide range of uncertainties. Secondly, the range of uncertainties considered is expanded through the use of multiple models, which thereby capture broader alternative scenarios and model structures. For example, SMOM models the fishery as an "inferior" competitor and thereby differs from Foosa in which the predators and the fishery are modeled as "equal" competitors for krill. Moreover, the SMOM model version presented here assumes no movement of krill between regions, whereas Foosa focuses on alternative movement scenarios. Earlier work (Watters et al. 2005, 2006, Plagányi and Butterworth 2007) highlighted the importance of checking the robustness of model conclusions to a wide range of assumptions for the rate at which krill is transported into the Scotia Sea: if the rate of krill transport is increased it is obvious that the demands of predators may be met in a SSMU even when static mass balance calculations suggest otherwise.

Concluding Remarks

Many of the theories in ecology are expressed in terms of mathematical models. As knowledge of ecological systems advances, so more and more details are integrated into the models. However, representing the full complexity of natural processes leads to mathematical models that may be intractable and usually give rise to parameter estimation difficulties, and hence the art resides in finding the right trade-off between biological complexity and mathematical tractability.

The field of quantitative fisheries stock assessment encompasses this philosophy in that it has developed to provide a scientific basis for the sustainable utilization of renewable resources. In narrowing its focus, fisheries modeling has developed some innovative and functional techniques (Sainsbury et al. 2000, Butterworth 2007, Smith et al. 2007), which have not yet diffused across to other terrestrial ecology fields (Milner-Gulland et al. 2010). We suggest these techniques could be developed and used in other research areas and systems, particularly given the relatively recent shift in focus from single-species to ecosystem modeling approaches that is mirrored in other ecological modeling.

Acknowledgments

We are grateful to the South African National Antarctic Program (SANAP) and National Research Foundation (NRF) which provided a research grant to fund this work and E. Plagányi's attendance at CCAMLR's 2005–2008 WG-EMM and WG-SAM meetings. We thank David Ramm of the CCAMLR Secretariat for providing the data needed. We also thank Mitsuyo Mori, Robin Thomson, Rebecca Rademeyer, George Watters, and members of the CCAMLR working groups on Statistics, Assessments and Modelling, and on Ecosystem Monitoring and Management for their contributions in laying much of the foundation upon which this work is built. André Punt and an anonymous reviewer provided helpful comments and suggestions.

Literature Cited

Alonzo, S. H., P. V. Switzer, and M. Mangel. 2003. An ecosystem-based approach to management: using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging. Journal of Applied Ecology 40:692–702.

Atkinson, A., R. S. Shreeve, A. G. Hirst, P. Rothery, G. A. Tarling, D. W. Pond, R. E. Korb, and E. J. Murphy. and J. L. Watkins. 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex and maturity stage. Limnology and Oceanography 51:973–987.

Boyd, I. L., J. P. Croxall, N. J. Lunn, and K. Reid. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life histories. Journal of Animal Ecology 64:505–518.

Butterworth, D. S. 2007. Why a management procedure approach? Some positives and negatives. ICES Journal of Marine Science 64:613–617.

Butterworth, D. S., A. Brandao, C. L. de Moor, and W. Robinson. 2011. Claim by Pichegru et al. that marine no-take zone benefits penguins remains premature. Ecology Letters. http://rsbl.royalsocietypublishing.org/content/6/4/498.abstract/reply#roybiolett_el_82

Butterworth, D. S., G. R. Gluckman, R. B. Thompson, S. Chalis, K. Hiramatsu, and D. J. Agnew. 1994. Further computations of the consequences of setting the annual krill catch limit to a fixed fraction of the estimate of krill biomass from a survey. CCAMLR Science 1:81–106.

Butterworth, D. S., and É. E. Plagányi. 2004. A brief introduction to some multi-species/ecosystem modelling approaches in the context of their possible application in the management of South African fisheries. African Journal of Marine Science 26:53–61.

Butterworth, D. S., and A. E. Punt. 1999. Experiences in the evaluation and implementation of management procedures. ICES Journal of Marine Science 56:985–998.

CCAMLR [Commission for the Conservation of Antarctic Marine Living Resources]. 2006. Report of the workshop on management procedures, Walvis Bay, Namibia, 17–21 July 2006. WG-EMM-06/40. CCAMLR, Hobart, Australia.

CCAMLR [Commission for the Conservation of Antarctic Marine Living Resources]. 2008. Report of the working group on ecosystem monitoring and management, St. Petersburg, Russia, 23 July–1 August 2008. SC-CCAMLR-XXVII/3. CCAMLR, Hobart, Australia.

Constable, A. J. 2006*a*. Setting management goals using information from predators. Pages 324–346 *in* I. L. Boyd, S. Wanless, and J. Camphuysen, editors. Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, UK.

Constable, A. J. 2006*b*. Using the EPOC modelling framework to assess management procedures for Antarctic krill in Statistical Area 48: evaluating spatial differences in productivity of Antarctic krill. Workshop document presented to WG-EMM subgroup of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), WG-EMM-06/38. CCAMLR, Hobart, Australia.

Crawford, R. J. M., P. J. Barham, L. G. Underhill, L. J. Shannon, J. C. Coetzee, B. M. Dyer, T. M. Leshoro, and L. Upfold. 2006. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. Biological Conservation 132:119–125.

Croxall, J. P., K. Reid, and P. A. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Marine Ecology Progress Series 177:115–131.

Doidge, D. W., J. P. Croxall, and J. R. Baker. 1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazelle* at South Georgia. Journal of Zoology 202:449–460.

Field, J. C., A. D. MacCall, R. W. Bradley, and W. J. Sydeman. 2010. Estimating the impacts of fishing on dependent predators: a case study in the California Current. Ecological Applications 20:2223–2236.

Fournier, D. A., H. J. Skang, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maundes, A. Nelson, and J. Sibert. 2011. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software. http://dx.doi.org/10.1080/10556788.2011.597854

Francis, R. I. C. C. 1993. Monte Carlo evaluation of risks for biological reference points used in New Zealand fishery assessments. Pages 221–230 *in* S. J. Smith, J. J. Hunt, and D. Rivard, editors. Risk evaluation and biological reference points for fisheries management. Canadian Special Publications in Fisheries and Aquatic Science 120.

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2003. Effect of complexity on marine ecosystem models. Marine Ecology Progress Series 253:1–16.

Hewitt, R. P., et al. 2002. Setting a precautionary catch limit for Antarctic krill. Oceanography 15:26–33.

Hewitt, R. P., G. Watters, P. N. Trathan, J. P. Croxall, M. E. Goebel, D. Ramm, K. Reid, W. Z. Trivelpiece, and J. L. Watkins. 2004. Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. CCAMLR Science 11:81–97.

Hill, S., J. Hinke, É. E. Plagányi, and G. Watters. 2008. Reference observations for validating and tuning operating models for krill fishery management in area 48. Workshop document presented to WG-SAM subgroup of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), WG-SAM-08. CCAMLR, Hobart, Australia.

Hill, S., E. J. Murphy, K. Reid, P. N. Trathan, and A. J. Constable. 2006. Modelling Southern Ocean ecosystems: krill, the food-web, and impacts of harvesting. Biological Reviews 81:581–608.

Hill, S., K. Reid, S. Thorpe, J. Hinke, and G. Watters. 2007. A compilation of parameters for ecosystem dynamics models of the Scotia Sea, Antarctic Peninsula region. CCAMLR Science 14:1–25.

Hill, S., P. N. Trathan, and D. J. Agnew. 2009. The risk to fishery performance associated with spatially resolved management of Antarctic krill (*Euphausia superba*) harvesting. ICES Journal of Marine Science 66:2148–2154.

Lander, M. E., T. R. Loughlin, M. G. Logsdon, G. R. van Blaricom, B. S. Fadely, and L. W. Fritz. 2009. Regional differences in the spatial and temporal heterogeneity of oceanographic habitat used by Steller sea lions. Ecological Applications 19:1645–1659.

Milner-Gulland, E. J., C. Edwards, A. Nuno, L. Palazy, S. Reljic, P. Riera, and T. Skrbinsek. 2010. New directions in management strategy evaluation through cross-fertilization between fisheries science and terrestrial conservation. Biology Letters. http://dx.doi.org/10.1098/rsbl.2010.0588

Mori, M., and D. S. Butterworth. 2006. A first step towards modelling the krill–predator dynamics of the Antarctic ecosystem. CCAMLR Science 13:217–277.

Pichegru, L., D. Grémillet, R. J. M. Crawford, and P. G. Ryan. 2010. Marine no-take zone rapidly benefits endangered penguin. Biology Letters 6:498–501.

Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper No. 477. Food and Agriculture Organization of the United Nations, Rome, Italy.

Plagányi, É. E., and D. S. Butterworth. 2005. Indirect fishery interactions. Pages 19–46 *in* J. E. Reynolds, W. F. Perrin, R. R. Reeves, S. Montgomery, and T. J. Ragen, editors. Marine mammal research: conservation beyond crisis. Johns Hopkins University Press, Baltimore, Maryland, USA.

Plagányi, É. E., and D. S. Butterworth. 2007. A spatial multi-species operating model of the Antarctic Peninsula krill fishery and its impacts on land-breeding predators. Workshop document presented to WG-SAM subgroup of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), WG-SAM-07/12. CCAMLR, Hobart, Australia.

Plagányi, É. E., and D. S. Butterworth. 2008. An updated description and parameterisation of the spatial multi-species operating model (SMOM). Workshop document presented to WG-SAM subgroup of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), WG-SAM-08/17. CCAMLR, Hobart, Australia.

Punt, A. E., and D. S. Butterworth. 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 Cape hakes (*Merluccius capensis* and *M. paradoxus*). South African Journal of Marine Science 16:255–285.

Rademeyer, R. A., É. E. Plagányi, and D. S. Butterworth. 2007. Tips and tricks in designing management procedures. ICES Journal of Marine Science 64:618–625.

Reid, K., and J. P. Croxall. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proceedings of the Royal Society 268:377–384.

Rose, K. A., et al. 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 2:115–130.

Sainsbury, K. J., A. E. Punt, and A. D. M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. ICES Journal of Marine Science 57:731–741.

SC-CAMLR. 1990. Report of the Ninth Meeting of the Scientific Committee for the Conservation of Antarctic Marine Living Resources. CCAMLR, Hobart, Australia.

Smith, A. D. M., E. J. Fulton, A. J. Hobday, D. C. Smith, and P. Shoulder. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. ICES Journal of Marine Science 64:633–639.

Smith, A. D. M., K. J. Sainsbury, and R. A. Stevens. 1999. Implementing effective fisheries-management systems: management strategy evaluation and the Australian partnership approach. ICES Journal of Marine Science 56:967–979.

Stokes, D., and P. D. Boersma. 2000. Nesting density and reproductive success in a colonial seabird, the Magellanic Penguin. Ecology 81:2978–2891.

Taylor, B. L., S. J. Chivers, J. Larese, and W. F. Perrin. 2007. Generation length and percent mature estimates for IUCN assessments of cetaceans. Administrative Report LJ-07-01. National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, California, USA.

Watters, G. M., J. T. Hinke, and S. Hill. 2008. A risk assessment to advise on strategies for subdividing a precautionary catch limit among small-scale management units during stage 1 of the staged development of the krill fishery in Subareas 48.1, 48.2 and 48.3. CCAMLR document WG-EMM-08/30. CCAMLR, Hobart, Australia.

Watters, G. M., J. T. Hinke, K. Reid, and S. Hill. 2005. A krill-predator-fishery model for evaluating candidate management procedures. CCAMLR document WG-EMM-05/13. CCAMLR, Hobart, Australia.

Watters, G. M., J. T. Hinke, K. Reid, and S. Hill. 2006. KPFM2, be careful what you ask for—you just might get it. CCAMLR document WG-EMM-06/22. CCAMLR, Hobart, Australia.

Wolf, N., and M. Mangel. 2008. Multiple hypothesis testing and the declining-population paradigm in Steller sea lions. Ecological Applications 18:1932–1955.

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. Journal of Animal Ecology 67:635–658.

Supplemental Material

Appendix A

Multispecies operating model (SMOM) equations (*Ecological Archives* A022-041-A1).

Appendix B

Leslie matrix computation of life history parameters (*Ecological Archives* A022-041-A2).

Appendix C

Catch data for fish (*Ecological Archives* A022-041-A3).

Appendix D

Reference observations from Hill et al. (2008) for validating and tuning operating models for krill fishery management (*Ecological Archives* A022-041-A4).