FISH and FISHERIES



FISH and FISHERIES, 2016, 17, 1152-1174

Necessary elements of precautionary management: implications for the Antarctic toothfish

Peter A Abrams¹, David G Ainley², Louise K Blight³, Paul K Dayton⁴, Joseph T Eastman⁵ & Jennifer L Jacquet⁶

¹Department of Ecology & Evolutionary Biology, University of Toronto, 25 Harbord St., Toronto, ON, Canada, M5S 3G5; ²H. T. Harvey and Associates, 983 University Ave., Los Gatos, CA, 95032, USA; ³Procellaria Research & Consulting, 944 Dunsmuir Rd., Victoria, BC, Canada, V9A 5C3; ⁴Scripps Institute of Oceanography, Mail Code 0227, La Jolla, CA, 92037-0227, USA; ⁵Department of Biomedical Sciences, Ohio University, Athens, OH, 45701, USA; ⁶Department of Environmental Studies, New York University, 285 Mercer St., New York, NY, 10003, USA

Abstract

We review the precautionary approach to fisheries management, propose a framework that will allow a systematic assessment of insufficient precaution and provide an illustration using an Antarctic fishery. For a single-species fishery, our framework includes five attributes: (1) limit reference points that recognize gaps in our understanding of the dynamics of the species; (2) accurate measures of population size; (3) ability to detect population changes quickly enough to arrest unwanted declines; (4) adequate understanding of ecosystem dynamics to avoid adverse indirect effects; and (5) assessment of the first four elements by a sufficiently impartial group of scientists. We argue that one or more of these elements frequently fail to be present in the management of many fisheries. Structural uncertainties, which characterize almost all fisheries models, call for higher limit points than those commonly used. A detailed look into the five elements and associated uncertainties is presented for the fishery on the Antarctic toothfish in the Ross Sea (FAO/CCAMLR Area 88.1, 88.2), for which management was recently described as 'highly precautionary'. In spite of having features that make the Ross Sea fishery ideal for the application of the precautionary approach, gaps in our knowledge and failure to acknowledge these gaps mean that current regulation falls short of being sufficiently precautionary. We propose some possible remedies.

Keywords *Dissostichus mawsoni*, precautionary approach, reference point, Ross Sea, stock–recruitment relationship, uncertainty

Correspondence:

Peter A Abrams,
Department Ecology
& Evolutionary Biology, University of
Toronto, 25 Harbord
St., Toronto, ON,
Canada M5S 3G5
Tel.: 416-978-1014
Fax: 416-978-8532
E-mail: peter.
abrams@utoronto.ca

Received 14 Dec 2015 Accepted 29 Mar 2016

Introduction	1153
Five requirements for a precautionary approach in a fishery	1154
(1) Target population size and its relationship to uncertainty	1155
(2) Accuracy of population estimates	1158
(3) Ability to detect and respond to population declines	1158
(4) Lack of negative ecosystem effects	1158
(5) Independence of science from policy making	1159
Can any system have adequate precaution?	1159
The regulation of the Ross Sea toothfish fishery: Ideal precautionary management?	1160

1152 DOI: 10.1111/faf.12162 © 2016 John Wiley & Sons Ltd

The five elements of precaution re-examined for Antarctic toothfish	1161
Is the target abundance appropriate?	1162
How well do we know population size?	1163
Can management respond rapidly to unexpected population declines?	1165
Is Antarctic toothfish harvest precautionary with respect to ecosystem effects?	1167
Is current management sufficiently impartial?	1168
What should be done?	1168
Acknowledgements	1169
References	1169

Introduction

Even well-meaning attempts to exploit responsibly may lead to disastrous consequences' – Ludwig, Hilborn and Walters (1993)

The Oxford English Dictionary defines 'precaution' as 'A measure taken in advance to prevent something dangerous, unpleasant, or inconvenient from happening'. Many have argued for a 'precautionary approach' to a variety of policy questions in fields ranging from approval of pharmaceuticals to exploitation of natural resources. The need for precaution arises in these fields because the outcome of the policy decision in question is uncertain, and some of the potential outcomes are very undesirable. Of particular concern are outcomes that threaten the future attainability of an optimal outcome (O'Riordan and Cameron 1995). In most cases involving human exploitation of natural resources, precaution entails limiting exploitation to prevent reaching excessively low levels of the resource. Dayton (1998) proposed that demonstrating lack of endangerment to biological systems be a prerequisite for approving fisheries regulations.

The widespread call for precautionary approaches coexists with disagreement over the exact measures that constitute such an approach, and about how much precaution is optimal. Differences of opinion on the meaning of a 'precautionary approach' have characterized most fields where it has been applied. This is likely the case because setting an optimal level of precaution requires agreement on how to weigh several very different goals, about which there are often legitimate differences in opinion. However, some claims that a precautionary approach is being followed are questionable. Some precautionary features are present in almost every scenario where the term has been suggested, but this should not allow the general designation to be used when other necessary features are missing.

The two main sources of uncertainty in determining the optimal level of precaution are the extent of foregone benefits (short-term profits. reduced disease burden, etc.), and both the costs and the relative probabilities of potential negative outcomes (long-term profits, increased scientific knowledge, etc.) under different policies. Foregone benefits are usually better known than costs. Much of the debate over precaution stems from the fact that the probabilities of the highly negative outcomes under various policy options are so poorly understood that quantitative calculation of the probability of various outcomes is impossible. In such cases, as pointed out by Richards and Maguire (1998, p. 1547), 'Under the precautionary approach, very conservative management measures are required when there is little scientific basis for advice'.

The need for more conservative measures can be assessed by examining a standard set of questions that apply to any context in which a dynamic system is being altered by a human activity; that activity has some direct benefits, but also contains significant risks of changing the system in an undesirable way. Climate change is a wellknown example (Weitzman 2009; Millner et al. 2013). In all such cases, the goal of avoiding highly undesirable outcomes requires: (1) limiting the intensity of human activities potentially causing negative effects, with limits based on knowledge of system dynamics and the associated uncertainties (here, the activity is greenhouse gas emissions); (2) an ability to assess the current state of the system (values of greenhouse gas concentrations and their rates of change) and uncertainties in those assessments: (3) a plan for and

an ability to alter the human activity (global emissions) rapidly enough to achieve item (1); (4) avoidance of adverse consequences to natural systems and species as the result of the changes (including both the emission rates and the measures taken to reduce them); (5) periodic review and assessment of the first four elements by scientists, at least a significant number of whom have not been directly involved in designing or approving the past policies governing the activity in question. The first four elements are necessary to achieve the goal of preserving the system under consideration. The fifth element specifies the source of evidence used to determine whether the first four elements are being satisfied by an ongoing activity. The major impediment to instituting precautionary approaches to climate change is element (3); the difficulty lies in getting most contributing entities (e.g. nations) to adopt effective plans, rather than in an inability to specify such a plan. There is some disagreement on how to deal with the uncertainties that affect element (1); see Weitzman (2009) and Millner et al. (2013). Element (5) has been carried out by the UN Intergovernmental Panel on Climate Change.

The preceding framework can also be applied to assessing putatively precautionary approaches in natural resource exploitation; here, we consider fisheries management. In this case, the negative outcomes to be avoided are collapse of the fished populations or adverse changes in other components of their ecosystems as a result of harvesting. The precautionary approach has been interpreted as meaning that '...the absence of adequate scientific information can no longer be a reason for postponing or failing to take conservation measures' (Richards and Maguire 1998, p;. 1545). The approach has already influenced fisheries regulations at a national level (e.g. the Magnuson-Stevens Conservation and Management Act in the USA: Restrepo 1999; Rosenberg et al. 2006) and international levels (e.g. the 1995 UN Agreement on Straddling and Highly Migratory Stocks: discussed in Longhurst 2010). In all of these cases, restraints on exploitation were deemed necessary to achieve sustainability of exploitation and to prevent undesirable changes in the ecosystem. Such restraints are made necessary by the exceptional ability of humans to over-exploit other species (Darimont et al. 2015). The fact that a large number of stocks still do not satisfy the population targets specified under existing policies that are labelled as precautionary (Neubauer *et al.* 2013) means that insufficient precaution has frequently not been recognized as such.

The remainder of this article begins with an interpretation of the above five elements of a precautionary approach in the context of fisheries. We argue that there are major uncertainties associated with the first four elements, and the fifth is frequently not satisfied. The last half of the article is a more detailed examination of the apparent failure to implement these five elements in a fishery that would appear to be ideally suited to a precautionary approach; the regulation of this fishery was recently proclaimed to actually have such an approach by ten fishery scientists (Hanchet et al. 2015a). This is the fishery for the Antarctic toothfish (Dissostichus mawsoni, Nototheniidae) in the Ross Sea. We end with some suggestions on how to increase precaution in both this fishery and in fisheries management more generally.

Five requirements for a precautionary approach in a fishery

Previous discussion of a precautionary approach in fisheries include: Lauck et al. (1998), Hutchings (2000), Mace (2001), Hilborn et al. (2001), Rosenberg (2002), Ludwig (2002), Hsieh et al. (2006), Clark (2010) and Longhurst (2010) among many others. Here, we concentrate on a framework that will allow a systematic assessment of insufficient precaution. This is best illustrated by a more detailed description of the preceding list of five elements of a precautionary approach as it pertains to a fishery that exploits a single species.

Element (1) specifies that there should be a target population size and/or a corresponding maximum fishery-caused mortality rate of the harvested species. These have been termed biological reference points; they are based on at least some ability to predict future dynamics and are ideally set at levels that do not greatly increase the probability of stock collapse. Defining 'collapse' itself requires some understanding of the adverse effects of low population sizes. This first element also requires a realistic recognition of uncertainty in such predictions of future population states, and upwards adjustment of the target in the light of the uncertainties. If size-selective harvesting occurs, sets of permissible size-specific harvest rates may have to be determined. Element (2) means that the population must be quantified frequently

and censuses must be reasonably accurate and unbiased, with acknowledgement of potential biases and uncertainties. Element (3) implies that reductions in fishing can be rapidly imposed and have the potential to restore the population size to above the limit point if the current census indicates that it has fallen or is about to fall below that level. Element (4) means that the predicted range of population size vs. time trajectories under the policy should not cause undesirable changes in other species or ecosystem properties. Finally, element (5) means that scientists involved in gathering ecological data and making population projections should be independent of entities or decision-makers who benefit from continuation (or discontinuation) of past policies; ideally, their work should be evaluated by other scientists who have not been involved in developing those policies. Each of these five elements has received some attention from fishery scientists, and one or more has been shown to be involved in many previous failures of precautionary fishing.

(1) Target population size and its relationship to uncertainty

Precaution seeks to avoid collapse or extinction of fish populations; this preserves the stock for sustainable exploitation or other future uses. As Lande et al. (1997, p. 1341) point out, 'Thresholds [population sizes below which harvest is prohibited] are a necessary feature of any harvesting strategy with the objective of minimizing risks of resource depletion or extinction, while optimizing yields'. The target abundance should be high enough to avoid local extinction or a prolonged period of low density (collapse). The most common upper limits of population size associated with collapse range from 20% down to 10% of the stock's 'original' biomass (Hutchings and Reynolds 2004; Reynolds et al. 2005). However, even 10% has been argued to be a safe level for some species (Hilborn 2002). Nevertheless, environmental variability implies that, over the long term, probabilities of extinction or collapse of a population are considerably higher at 10-20% than at 50% of original abundance (Lande et al. 1997; see Dulvy et al. 2003 for a discussion of marine extinctions). 'Original' biomass is most often considered to be biomass when first measured, which is generally less than what prevailed prior to human exploitation (Hutchings and Reynolds 2004); in most

cases we don't know how much less. 'Original' can also refer to biomass in the unfished state, which can be considered to be the current carrying capacity of the population. The threshold for cessation of harvesting must be significantly above the value chosen to define depletion or collapse (see VanderZwaag et al. 2012; box 1, figure 2). Because environments are variable, system dynamics are poorly known, perfect control of exploitation rate is usually not possible, and populations are difficult to census, preventing unacceptably low population sizes requires setting the target population at a considerably higher level than would otherwise be the case. There is no fishery for which current knowledge allows an exact calculation of probabilities of 'collapse' within different time frames, given any particular harvest policy (or no harvest at all). This has led to various proposals for minimum population sizes.

Nevertheless, there is currently some degree of consensus on a rough definition of the target density. Following the 1996 Magnuson-Stevens Act in the US and the 2002 UN Summit on Sustainable Development, an adult biomass that produces maximum sustainable yield (MSY) has become the target adult population size for many systems (Neubauer et al. 2013; see also Froese and Proelss 2010, 2012, 2013; Agnew et al. 2013). The MSY population by definition has the greatest expected population growth rate, which seems to suggest that rapid recovery should occur from that size. There are at least three major problems with this logic. The first is that the MSY population size is seldom if ever a known quantity, and it is one that is likely to shift over time because of both environmental (e.g. Clark et al. 2003; MacCall et al. 2012) and fishery-induced evolutionary change (e.g. Belgrano and Fowler 2013; Laugen et al. 2014; Dunlop et al. 2015). The second is that MSY does not measure the sensitivity of the population to additional mortality; in a variety of simple food web models, MSY can occur at a per capita fishery mortality rate (F) very close to that which, if maintained, would guarantee extinction (Abrams 2009a,b,c; Abrams et al. 2012). As a consequence, as Mace (2001) and others have noted, B_{MSY} (or the corresponding fishing mortality rate F_{MSY}) is often not sufficiently precautionary. The third issue is that populations above B_{MSY} are generally preferable both in economic terms and for avoiding collapse (e.g. Beddington et al.

2007). These three problems are explained in greater detail below.

How well do we know MSY? The MSY abundance is determined by density-dependent feedbacks to population growth of a focal species, due to both intraspecific interactions and changes in the abundances of other species at both higher and lower trophic levels. The feedbacks via food web changes can take considerable time to occur (Yodzis 1988) and have not been studied for the vast majority of harvested species. The current guesses about MSY abundance are usually based upon temporal correlations of stock size and subsequent recruitment into the breeding population. In most cases where the data exist, there is no statistically significant increasing relationship. Szuwalski et al. (2015) found no relationship for 61% of the 224 stocks in the revised Myers et al. (1999) database updated by Ricard et al. (2012). Ludwig (1998) had earlier made the same point. This lack of relationship does not imply a high ability to rebound from very low population sizes, both because of the frequent lack of data at low stock sizes and the near universal absence of data on the abundances of interacting species affecting the growth of a particular stock.

Hilborn (2010) and others have argued that these data support a Beverton-Holt (B-H) model for the stock-recruitment relationship (SRR) with a steepness parameter (h) on the order of 0.7 for an average species. Both the preference for the B-H model and the high h value follow from the lack of a clear relationship; such a model is good at fitting a horizontal line when data from low values of the variable are scarce. Szuwalski et al. (2015) conclude that other environmental and community ecological variables are likely to have larger effects on recruitment than its spawning stock size. The actual shape of the relationship is likely to be determined by the recent abundances of a variety of other species; for example, food organisms and predators of larval, juvenile and subadult fish. Other work supporting this conclusion is discussed under point (4) below. In stocks with short life spans and a long recorded history of exploitation, surplus production models can be used to estimate MSY based on catch and effort data, but there are also uncertainties associated with this approach.

There appears to be no theory showing if or when the combination of intraspecific and community feedback processes actually produce a MSY abundance that is close to what would be obtained

by fitting a B-H model to the stock-recruitment measurements obtained in a stochastic environment. SRR models in general are not adequate for representing the types of interactions that are likely to occur between different juvenile sizeclasses in the context of species with very high ages of maturation. In most cases, B-H relationships are only chosen in preference to one or two other forms. Yeakel and Mangel (2015) show that the B-H relationship represents a very special case within a much broader gradient of plausible SRRs. Consumer-resource models only lead to something approximating a B-H relationship for the consumer species in rather special circumstances (Abrams 2009a,b,c); these models also frequently predict MSY population sizes relatively close to the unfished size. MacCall (2002) noted that large predators were expected to have MSY at >50% of baseline in food webs where they have smaller competitors.

The assumption that a B-H SRR can be used to model population growth is particularly problematic when populations actually experience reduced per capita growth at low densities. A variety of mechanisms can produce such Allee effects (depensation), including difficulty of finding mates, a breakdown of mating behaviours, shifts in size-structure and shifts in community composition at low densities (Walters and Kitchell 2001; Abrams 2011; DeRoos and Persson 2013). Recent work has shown that a number of heavily exploited fish exhibit such Allee effects, a finding that is strictly incompatible with the B-H model (Hutchings 2014, 2015). Other meta-analyses have suggested that Allee effects are uncommon (Hilborn et al. 2014). However, if most Allee effects are brought about by community ecological shifts, they may only be observed when the low density is maintained for a long enough time for these shifts to occur; this may account for the correlation of time at low density and limited recovery noted by Neubauer et al. (2013). It is also likely that immigration from non- or lessexploited populations of a particular species obscures the presence of Allee effects in heavily exploited populations of some species. Hutchings (2015) notes that scarcity of conclusive empirical demonstrations of Allee effects may be due to the paucity of time-series data with low population sizes. He argues that an impaired-recovery threshold population of 10% of the maximum population is prudent.

Assuming density dependence based on a B-H stock–recruitment relationship is decidedly non-precautionary, in that it produces relatively low MSY populations relative to many other potential relationships or models, that is $\leq 50\%$ of unharvested biomass. The 50% upper limit is strictly true for a continuous form of the B-H model lacking population structure (Mangel *et al.* 2013; eq. (4)) and appears to be true of the age-structured stochastic models with B-H SRRs that were explored by Hilborn (2010).

Thus, we generally don't know (even approximately) the MSY size for most species, although MSY population sizes ≤50% may be more common than >50%; Hilborn (2010) argues this is true for exploited fish species, and it may also be true of many other animal taxa (Sibly et al. 2005). Some models of population growth predict MSY densities below one-half of the equilibrium abundance of the unharvested population. This is true of the Pella and Tomlinson (1969) model for a densitydependent exponent <1. It is also true for consumer species in wide range of consumer-resource systems having resources that do not reproduce themselves (Abrams 2009a,b,c). However, both Pella-Tomlinson models with larger exponents and a wide range of food web models predict MSY population sizes is greater than half the unfished equilibrium. Both Sibly et al.'s (2005) general analysis of empirical studies of density dependence and Thorson et al.'s (2012, their fig. 2) analysis of exploited fish stocks find that a sizable minority of fish species have MSY populations above one-half carrying capacity. Unfortunately, for any randomly chosen harvested species we lack the data that would provide a reliable estimate of its MSY size, much less how it would change with evolution or altered environmental variables.

The second issue with MSY-based targets is that maintaining a population close to its MSY abundance can create a large risk of collapse when $F_{\rm MSY}$ is large enough that the sum of per capita natural and fishing mortalities is close to the maximum per capita reproductive rate. This is actually true for a wide range of parameter values for the predator species in simple predator–prey models having standard functional components (Abrams 2009a,b,c). How large a fishing mortality is too large is again difficult to determine. A high $F_{\rm MSY}$, particularly one that is at least comparable to natural mortality, means that stock size could drop rapidly if the environment changed in a manner

that significantly reduced the per capita recruitment rate or increased natural mortality (e.g. MacCall et al. 2012). Walters and Martell (2002) argue against a variety of simple formulas for maximum fishing mortality and suggest that fishing mortality should be much less than natural mortality for most stocks. A later meta-analysis (Zhou et al. 2012) suggested that F_{MSY} is close to natural mortality (M) for many teleost species, but on average <M/2 for chondrichthyans, with a mean of approximately M/3 for Carcharhiniformes. As noted elsewhere, estimates of both M and F_{MSY} are associated with major uncertainties. Because natural mortality is temporally variable, a high value of F that is safe under average conditions may cause a collapse during a time period with unusually high natural mortality. In general, more variable populations require higher mean target densities or lower maximal catch rates (Lande et al. 1995, 1997; Roughgarden and Smith 1996).

The third issue mentioned above was that population sizes greater than MSY are usually preferable in economic terms. This is not a new observation (e.g. Beddington et al. 2007; Grafton et al. 2007), and it can arise because the higher abundance allows a given catch to be achieved with lower cost. Moreover, given an allowable catch that is set higher than it should be, populations above MSY decline at a decreasing rate over time, while those at or below MSY will decline at an accelerating rate. This makes sizes above MSY more resilient. Even if sustainable profits are reduced for population sizes above MSY, the reduction will be relatively small for a wide range of population sizes. Thus, Hilborn (2010), who suggested that MSY population size is frequently close to 30% of original biomass, also concluded that 50% of original biomass usually lies within the range of population sizes producing high enough ('pretty good') yields and was generally preferable to 30%.

All of the above has ignored the impact of fishery-induced evolution on both the MSY population size and the resistance of the stock to future changes in natural mortality. It is known that such evolutionary effects occur and that they should often affect the density-dependent processes that determine MSY (Kuparinen *et al.* 2014). Nevertheless, we are currently unable to make quantitative predictions on their time course in the vast majority of stocks (Jorgensen *et al.* 2007; Engen

et al. 2014; Dunlop et al. 2015). Because such evolutionary responses typically involve reduced body size at maturity, they are likely to affect the MSY fishing intensity when targets are expressed in terms of biomass. There is evidence that higher mortality magnifies population variability in some exploited fish species (Hsieh et al. 2006), which again would argue for lower MSY mortality rates than those predicted by models lacking environmental fluctuations.

Given our limited knowledge of the dynamics and effective form of density dependence of most exploited fish species, a precautionary assumption for a species lacking adequate stock-recruitment data would seem to be a target equilibrium above 1/2 of the original abundance/biomass (B₀). Values above B₀/2 are especially important for long-lived species and/or species with low maximum reproductive rates, which are known to be particularly susceptible to collapse under harvesting (Reynolds et al. 2005: Neubauer et al. 2013). Roughgarden and Smith (1996) provided some general arguments for setting target densities for all fish at 75% of original levels. On the other hand, when there is a history of persistence in the face of exploitation at populations much lower than original biomass (e.g. New Zealand rock lobster *Iasus edwardsi* (Palinuridae) and snapper Pagrus auratus (Sparidae); Hilborn 2002), target densities lower than $B_0/2$ may be appropriate. However, even such cases should take into account the decreased ability to rebound observed in stocks that have been reduced for many years (Neubauer et al. 2013).

(2) Accuracy of population estimates

Marine fish are difficult to census (Hilborn 2002). Mark–recapture methods avoid some of the worst problems of catch per unit effort (CPUE) methods (Hutchings and Myers 1994), but potential errors are introduced by many factors, including inability to determine the effects of capture and tagging on both behaviour and mortality, as well as lack of information on the behavioural heterogeneity of the stock and the movement patterns of individuals. When the tag-recovery rate is low, random errors can produce misleading estimates over short time spans. In most cases we do not know enough to estimate confidence intervals on the population estimates. The presence of natural selection against behaviours that lead to capture is likely to

alter the meaning of tag-recovery rates over time in ways that are poorly understood. Scientific surveys that are independent of the fishing industry can provide better population estimates, but they are often expensive and difficult to design. This means that considerable uncertainty in the current state of the population is usually unavoidable, again arguing for conservative management.

(3) Ability to detect and respond to population declines

Populations do not change only because of fishing, and unexpected declines may occur because of poor recruitment conditions or raised natural mortality, particularly if these conditions persist over several years. A decline in the survival of early stages of a species having a long pre-adult period will not be noticed unless these stages are censused on a regular basis, and there will be a corresponding time lag in the resulting recruitment of adults. Depending on the length of the pre-adult period, the system may be committed to a number of years of decline in adults for a long period after the recruitment problem first becomes evident. Safina et al. (2005) attribute the recovery of Atlantic black sea bass (Centropristis striata, Serranidae), scup (Stenotomus chrysops, Sparidae), sea scallops (*Placopecten magellanicus*, Pectinidae), vellowtail flounder (Limanda ferruginea, Pleuronectidae) and king mackerel (Scomberomorus cavalla, Scombridae) to the rapid reduction in harvesting following evidence of low abundance. Rapid reduction of harvesting in turn requires timely knowledge that abundance has decreased or will decrease. It is also important that the adjustment of fishing effort based on current stock size not lead to instability in the dynamics of the exploited stock or produce extinction of other species that interact with the exploited one. Matsuda and Abrams (2013) discuss both of these possibilities.

(4) Lack of negative ecosystem effects

Mace (2001), Hilborn (2010), Constable *et al.* (2000) and many others mention ecosystem-level effects as a reason to set target densities for single species above their MSY stock size. This is based largely on the greater level of uncertainty that characterizes ecosystem-level effects. By definition such effects depend on knowledge of the population dynamics of many species as well as physical

and chemical variables. Even when the non-living variables are ignored, the resulting community ecology models have included a sufficiently high level of uncertainty that at least one prominent British ecologist has recommended abandoning efforts to describe population changes in a community context (Lawton 1999). Sainsbury *et al.* (2000, p.731) state what is by now obvious: 'Predicting the results of any management action is very uncertain because the dynamics of ecosystems are complex and poorly understood'.

These uncertainties have not inhibited calls for ecosystem models in fisheries, and the widespread use of a particular computer program to describe the dynamics of many systems (Ecopath with Ecosim (EwE); Christensen and Walters 2004). More recent years have seen the development of other programs designed for marine ecosystems (e.g. 'Atlantis', discussed in Fulton et al. 2011). Nevertheless, all of these modelling frameworks are mainly useful in revealing possibilities rather than making predictions (as admitted by Fulton et al. 2011). EwE did not fare well in one of the few comparisons of modelling frameworks for a particular system (Koen-Alonzo and Yodzis 2005). Plagányi and Butterworth (2004) and Abrams (2014) discuss other limitations of EwE, and Plagányi et al. (2014) argue instead for using a variety of models of intermediate complexity to determine the range of potential effects at an ecosystem level. Because there is limited knowledge of how to model trophic linkages in simple food web models (Abrams 2010), predictive results for large ecosystem models will necessarily have higher uncertainties. At the same time, empirical evidence has shown ecosystem-level effects of mortality on particular species in some large marine systems (e.g. Daskalov et al. 2007), so ignoring the possibility of such effects is not a realistic option. Analyses incorporating interspecific interactions have provided greater insight than singlespecies models in the few cases where multispecies data have been available (e.g. Hjermann et al. 2007). For most systems, such data are not available, and it is necessary to adopt relatively high target abundances to have a high probability of avoiding undesirable ecosystem changes.

(5) Independence of science from policy making

Conflicts of interest and intellectual biases are likely to inhibit some researchers from

acknowledging uncertainties and questioning results that are consistent with continued exploitation. Hutchings *et al.*'s (1997) analysis of government scientists' roles in the policies that are likely to have caused the cod collapse was mentioned above. Scientists need not have connections with industry to lack impartiality. The high fraction of stocks reduced by 80% or more (Hutchings and Reynolds 2004) argues that there has been a general tendency by fisheries regulators and many fishery scientists to overestimate the ability of fish populations to withstand intense harvest over long time periods.

Any area of science with unsettled theory and limited empirical work is likely to lead to different opinions being held by different investigators. Uncertainties are almost always underestimated by practitioners in a field, as is confirmed by a vast literature in economics (see Quiggin 2010). Underestimates of the level of uncertainty by definition lead to less than appropriate precaution. Independent of uncertainty, it is difficult for scientists to avoid favouring policies they have been involved in designing or approving. Similarly, strong previous positions against current policy will often lead to a bias against evidence that supports that policy. In such situations, it becomes important that proponents of opposing viewpoints have opportunities to respond directly to the arguments of the other side. MacCall et al. (2012), in a discussion of precautionary management, attribute success in managing Pacific sardine (Sardinops sajax, Clupeidae) in the California Current to intensive peer review. Broad engagement by all stakeholders, including unaffiliated scientists, is among the hallmarks of the best managed fisheries (Longhurst 2010).

Can any system have adequate precaution?

Under ideal circumstances, we would understand population and ecosystem dynamics well enough to justify a probability distribution of population trajectories under alternative harvesting policies. This could then be combined with quantitative measures of costs and benefits of each trajectory (Clark 2010). A policy involving targets and restorative actions when those targets are missed could then be negotiated between interested parties. This ideal is unlikely to be realized for many fisheries systems in the near future due to the high level of structural uncertainty in dynamical models of aquatic ecosystems (Schnute and Richards

2001). At a minimum, this requires consideration of multiple alternative models (e.g. Harwood and Stokes 2003; Hill et al. 2007). The currently popular ideas of 'management strategy evaluation' and 'management procedure' (Punt 2006) seek to achieve such an approach, but there is little agreement on how to deal with structural uncertainty in these frameworks, other than considering a number of alternative models (see Stewart and Martell (2015) for some recent ideas on interpreting analyses with an ensemble of models). The precautionary approach always implies that, given equal estimated probabilities of occurrence of two outcomes having equal magnitude but opposite deviations from the ideal, the negative deviation (associated with smaller population size or undesirable ecosystem shift) should be weighted more heavily. The same applies to the predictions of alternative models. However, given a profound lack of knowledge of system dynamics, deciding on exact weightings involves more than purely scientific considerations. Whatever procedure is used to weight outcomes or models, underestimation of uncertainties will lead to an overly high maximum harvest rate.

None of the above should be taken as an argument against all fisheries. Previous experience with recovery from low population size is one of the most reliable indications of the safety of subsequent reduction of the population. In many cases, a long history of fishing and fisheries research provides evidence of sustainability over at least the medium term. In other cases, the benefits to the human community may outweigh some increase in the risks of stock depletion or ecosystem effects. Loss of such benefits should be regarded as one of the potential negative effects of reducing harvests (Hilborn et al. 2001). However, it is obvious that whatever benefits accrue to humans will end if the stock declines sufficiently. Thus, in discussing precaution, Hilborn et al. (2001, p. 100), endorse an earlier UN FAO statement, '...where the likely impact of resource use is uncertain, priority should be given to conserving the productive capacity of the resource'. Clark (2010) and Grafton et al. (2008) have expressed similar sentiments.

The regulation of the Ross Sea toothfish fishery: ideal precautionary management?

Our case-study for assessing precautionary management involves the fishery for Antarctic

toothfish (Dissostichus mawsoni, Nototheniidae; hereafter AnT) in the Ross Sea region of the Southern Ocean. This species has been the subject of an 'exploratory' fishery that began in 1996-1997 in FAO Areas 88.1 and 88.2 (for maps see figs 1, 2 in Hanchet et al. 2015b) and is managed under the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). CCAMLR uses the classification 'exploratory' for fisheries lacking data that are normally used in developing a management strategy; this contrasts with 'established' fisheries (CCAMLR Conservation Measure 21–02; www.ccamlr.org/sites/drupal. ccamlr.org/files//21-02 29.pdf, 12 October 2015). The fish is generally marketed as 'Chilean Sea Bass', a term originally developed for its congener, D. eleginoides. Most of the analysis and modelling used in managing the AnT fishery is based on Area 88.1. where the majority of fish are caught. Data on the catch are provided by licensed commercial fishing vessels. The catch in Area 88.1 first exceeded 2000 t in 2004 (i.e. 2004-2005 season, the austral summer); in recent years the quota has been somewhat greater than 3000 t and the catch has closely approximated the quota for the past four years (CCAMLR 2014b). This annual harvest is assumed to be the production rate of the fish population at half its original abundance as currently estimated by those managing the fishery (CCAMLR 2013).

The outlines of CCAMLR's harvesting strategy for biological resources were presented in Constable et al. (2000), and its subsequent development is documented in CCAMLR (2004, 2011, 2012, 2013, 2014a,b,c). Laudatory reviews include Croxall and Nicol (2004), Kock (2007), and Constable (2011). In contrast, various aspects of the Ross Sea toothfish fishery have also been criticized (Blight et al. 2010; Jacquet et al. 2010; Ainley et al. 2013; Christian et al. 2013a,b; O'Brien and Crockett 2013; Abrams 2014; Ainley and Pauly 2014). In response, ten scientists, all of whom have had some involvement with AnT management, recently published a defence of the fishery and its management as being 'precautionary' (Hanchet et al. 2015a). However, we argue that their defence actually illustrates a lack of precau-

The fishery for AnT in the Ross Sea region is of particular relevance to assessing precaution because it represents a 'best case' scenario for such an approach. Unlike the majority of fisheries,

the actual catch has been effectively regulated, and typical problems associated with fleet overcapacity (Clark 2007) do not arise. Undetected illegal fishing vessels are thought to be rare (Mormede et al. 2014a); thus, the catch in most years probably does not exceed that specified in the regulations, which are updated annually. A Working Group on Fisheries Stock Assessment (WG-FSA) provides recommendations to the Scientific Committee, which in turn advises the CAMLR Commission, which decides on any changes to fishery policy. This multilayer process at least theoretically provides opportunity for critical review of the initial WG-FSA recommendations. The WG-FSA is in principle independent of the commercial interests that carry out the fishing. All of these regulatory features should favour precaution.

The societal and economic benefits from the AnT fishery are relatively small, another factor that should favour a precautionary approach. The majority of the AnT catch in most years has been taken by New Zealand flagged vessels (Ainley and Pauly 2014), but even for this nation, AnT does not rank in the top ten fisheries in terms of income generated or export value. (The tenthranked species' export value is NZ\$31 million of the total exports of NZ\$1.53B in 2014 for all fisheries. http://www.seafoodnewzealand.org.nz/ourindustry/key-facts/, 13 December 2015). Unemployment costs from a reduced fishery would be exceptionally small in a case like AnT, which involves only 15-25 vessels (flagged from several nations) operating over less than 2 months of the vear (CCAMLR 2013, 2014b). In addition, the status of the Ross Sea shelf and slope marine ecosystem, not long ago ranked as one of the areas on the planet least impacted by humans (Halpern et al. 2008), enhances its scientific value, which is likely to be diminished by fishing. The Ross Sea region is the only large area on Earth where seaice extent and season are increasing (Stammerjohn et al. 2012), thus providing the only natural laboratory remaining to understand the ecological implications of this trend. By changing the abundance of a major component of the ecosystem, harvesting AnT will complicate predictions of the effects of climate change on the system; see the 'ecosystem effects' section below. These facts should be considered in any calculation of net benefits of the harvest.

A final feature promoting a precautionary approach for AnT is that key elements of such an

approach are specified by a treaty signed by all nations legally participating in the fishery. The treaty also requires strict protection of other species that are part of the ecosystem. The outcomes to be achieved and avoided by any fishery are described by the CAMLR Convention Article II, paragraph 3: 'Any harvesting and associated activities in the area to which this Convention applies shall be conducted in accordance with the provisions of this Convention and with the following principles of conservation:

- Prevention of decrease in the size of any harvested population to levels below those which
 ensure its stable recruitment. For this purpose
 its size should not be allowed to fall below a
 level close to that which ensures the greatest
 net annual increment;
- Maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources and the restoration of depleted populations to the levels defined in subparagraph (1) above;
- 3. Prevention of changes or minimization of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades, taking into account the state of available knowledge of the direct and indirect impact of harvesting, the effect of the introduction of alien species, the effects of associated activities on the marine ecosystem and of the effects of environmental changes, with the aim of making possible the sustained conservation of Antarctic marine living resources'. (Text from: http:// www.ccamlr.org/en/organisation/camlr-convention-text#II, 15 December 2015). The preceding text is consistent with some recent discussions of precaution in fisheries in general (Clark 2007, 2010; Longhurst 2010).

The five elements of precaution re-examined for Antarctic toothfish

This section lays out the case that current harvest policy for AnT is insufficiently precautionary. The underlying problem with all of the optimistic CCAMLR (e.g. 2013, 2014b) predictions of the effects of AnT harvest on its population size is that the model on which both population size and dynamics are based (Mormede *et al.* 2014a) has important components (functional forms and

parameter values) that are either totally unknown, or can only be estimated with very large error bounds. These unknowns and errors have been ignored in making predictions and judging the uncertainties in those predictions. Ignoring such structural unknowns is a widespread problem of model-based predictions in biology (May 2004), fisheries in general (Schnute and Richards 2001; Longhurst 2010) and in the specific case of the AnT (Abrams 2014), May (2004) identifies this common practice as an 'abuse of mathematics'. In considering climate change policies, Weitzman (2009) pointed out that such structural uncertainties usually require an increase of the probabilities assigned to extreme outcomes in quantitative analyses of the consequences of a policy under consideration. In this case, the extreme outcomes are low population size and/or adverse effects on other species.

In the following review of elements (1)–(4), we pay particular attention to how the defence of the fishery by Hanchet *et al.* (2015a) responds to previous criticism. These responses provide a good indication of the presence or absence of impartiality in the scientific enterprise responsible for the current policy (i.e. element (5)).

Is the target population size appropriate?

Hanchet et al. (2015a) trace the current AnT fishery policy to the reinterpretation of the Convention proposed by Constable et al. (2000). The latter authors interpret point (1) of Convention paragraph 3, above, as meaning that the median (rather than minimum) stock size should be no lower than 50% of pre-harvest stock size for this species (and for Patagonian toothfish, D. eleginoides), while the minimum need only be greater than 20% of pre-harvest, and this minimum should have a <10% chance of occurring. Hanchet et al. (2015a) and CCAMLR have followed this reinterpretation, although there has been no published discussion of its merit. Other than a reference to Beddington and Cooke (1983), the basis for the reinterpretation of Convention point (1) is not presented in Constable et al. (2000) or in Constable (2011). Beddington and Cooke (1983) was a theoretical analysis based on an extremely simple model, whose assumptions have little correspondence to AnT. More recent work by Beddington et al. (2007, their figure 2) suggests that the economic costs of reducing populations below abundances associated with maximum yield (MSY) are usually greater than those of maintaining the population above MSY levels (see also Grafton *et al.* 2007).

The Convention's ecosystem requirements (2) and (3) were interpreted by Constable *et al.* (2000) as only requiring lower harvesting rates for species that formed the ultimate source of energy for higher trophic levels, so that Antarctic krill (*Euphausia superba* Euphausiidae) would be harvested down to 75% rather than 50% of initial biomass. This approach will be discussed later in the treatment of element four.

If ecosystem effects could be ruled out, the AnT target of 50% of initial biomass might be considered precautionary, provided this was also known to be at or above MSY and to involve a fishing mortality that was small relative to natural mortality. Neither of the latter two conditions is known to be satisfied here, and potential ecosystem effects are even less well understood. The MSY population size for Ross Sea AnT is unknown. There is no information on density dependence generally, or on the relationship between stock size and recruitment size. The time span over which any population data for Area 88.1 are available is approximately the length of the maturation time. The fact that AnT is exceptionally long-lived (to ~50) and slow-maturing (median age ~17 years for females; Hanchet et al. 2015b) argues for a conservative target population size. In their review of the status of harvested stocks, Reynolds et al. (2005, p. 2337) found that, 'The empirical evidence suggests that large body size and late maturity are the best predictors of vulnerability to fishing'.

The MSY population size is determined by density-dependent feedbacks; as noted above, in fisheries these are commonly assumed to be due solely to the SRR. The population projections made by CCAMLR have assumed a B-H SRR with a steepness parameter of h = 0.75 based on average figures from a subset of the Myers et al. (1999) database. Given our limited knowledge of AnT population dynamics, a precautionary approach cannot ignore the possibilities of a low steepness (h) within a B-H relationship, a non-B-H relationship, complete inadequacy of any standard SRR to represent density dependence (as in the case of an Allee effect), and/or an MSY SSB above half the original biomass. Another key parameter of any population model is the per capita

reproductive rate at very low densities, which enters into the SRR. This cannot be measured directly for AnT because of the absence of studies of spawning adults or small fish (Hanchet et al. 2008, 2015b; Ashford et al. 2012). If these become quantifiable in the future, it will take many years to accumulate an informative timeseries relating the two quantities, given the 17year female maturation period and significant environmental change currently underway in Area 88 (see below). The low-density reproductive rate used in the recent reports from the CCAMLR Fishery Stock Assessment working (CCAMLR 2011, 2012, 2013, 2014a,b) and recent population analyses by associated scientists (Mormede et al. 2014a,b; Hanchet et al. 2015a,b) is not presented in any of those documents. This is a key variable for assessing sustainability of any fishing pressure.

For the sake of argument, assume that an SRR describes all density dependence and that it is B-H. For the species judged to be ecologically similar to AnT in CCAMLR's analyses [details given in Dunn et al. (2006)], 25% of estimated h values are < 0.46. Abrams (2014) pointed out that this lower range implies quite different dynamics than the h = 0.75 that CCAMLR assumes for AnT. Hanchet et al. (2015a, p. 338) dismiss the importance of the difference between h values of 0.46 and 0.75. because these two parameters imply per capita recruitment rates that only differ by ~20% when the population is at their target abundance. However, this proportional difference rapidly increases as population size decreases. Because populations may have as much as a 10% chance of dropping to 20% of carrying capacity under the CCAMLR management scheme, recruitment at this population size is also important for precautionary management. Here, the per capita recruitment is proportional to h, so per capita recruitment is 39% lower if h = 0.46 than if h = 0.75. There is no reason to expect similar SRRs for the unique Antarctic fish fauna and the largely temperate and shorter lived species present in the Myers database. Even accepting the distribution of h values provided by Myers et al. (1999) for the 'similar' taxa identified by Dunn et al. (2006), there is a 25% chance that the value of h is actually <0.46, which would lead to a still lower population growth rate at 20% of initial biomass. The assumption of h = 0.75 would then lead to very significant overharvesting

approaching and below 50% of the estimated unharvested level. Of course, determining the chance that SSB will reach 20% of its unharvested size depends on the SRR (actually on the underlying community ecological processes that can sometimes be summarized by an SRR).

Population projections are also dependent on the estimated mortality rates. Because these, like population size estimates, depend on the mark–recapture programme described in Mormede *et al.* (2014a), they are considered in the following section.

How well do we know the population size?

In their defence of the AnT fishery, Hanchet et al. (2015a) cite Mormede et al. (2014a) as showing that the 2013 SSB is 75% of pre-exploitation level with 95% confidence intervals of 71-78% of B₀ (i.e. 51 530 t; confidence interval 48 860-53 680 t). This estimate is approximately 2000 t more than the 2011 estimate (CCAMLR 2011) of the 2009 SSB (49 580 t). Under the CCAMLR (2013, fig. A3) estimated biomass trajectory, the 2013 figure should have been approximately 6000 t less than that in 2009. If the 2013 figure and trajectory are correct, the 2011 estimate of the 2009 population was low by approximately 8000 t (i.e. 16%). Hanchet et al. (2015a) do not explain the high confidence in current estimates, given the discrepancy with earlier ones, as well as the discrepancy of two previous sets of population estimates with each other (Abrams 2014). Hurtado-Ferro et al. (2015) provide examples of some of the problems that can result from such 'retrospective patterns'.

In the absence of earlier (pre-1997) data, the estimation of pre-exploitation SSB is based on extrapolation from population estimates in later years using mark-recapture data, an assumed population growth model and a proprietary computer program (CASAL). These early estimates of population size necessarily are highly uncertain because very few tagged fish had been recovered (a total of 137 tags by the end of 2006; Mormede et al. (2014a)). We do not know whether the 1996 SSB was historically atypical. Given that some illegal exploitation (Österblom et al. 2010) and considerable alteration of hydrographic attributes had already occurred by 1997 owing to climate change in the Ross Sea region (e.g. Jacobs 2006; Jacobs and Giulivi 2010; Comiso et al.

2011; Stammerjohn et al. 2012), it seems more likely that the 1996 AnT population (and hence SSB) was lower than a pre-fishery median value. Given the important role of ocean circulation in the life history of this population (Ashford et al. 2012; Hanchet et al. 2015b), it is possible that changes in circulation predating 1997 (Jacobs 2006; Comiso et al. 2011) could have adversely affected population size. In any event, the current SSB relative to a meaningful pre-harvest average cannot be known with 95% confidence to within $\pm 20\%$, let alone the claimed limits of $\pm 3-4\%$. Given the uncertainties in the proper structure of a dynamic model, such narrow bounds are not credible.

Current AnT population estimates, based on mark-recapture, are subject to many sources of error, some discussed in Abrams (2014). These include nonrandom mixing of marked individuals. non-random sampling of the population by fishing vessels and unverified assumptions regarding the survival and behaviour of individuals and tags. Perhaps the most troubling source of error is the use of fishing vessels for the sampling programme. CCAMLR explains that this has been unavoidable, given the expense and the large spatial extent of the population involved; however, it means that random sampling cannot occur. The limited spatial modelling that has been done (Mormede et al. 2014b) has only considered random movement on a large spatial scale (between 24 000 km² cells). Very little is known about adaptive aspects of movement, interindividual variation in movement, or variation in population densities on a finer spatial scale. Random mixing is also unlikely on a smaller spatial scale, where fish are likely reacting to densities of prey, conspecifics and their own predators in unknown ways; as with other notothenioids, AnT change their spatial distribution with size (Gon and Heemstra 1990; Eastman 1993; Hanchet et al. 2008, 2015b). Depending on the spatial scale of movement and what determines movement behaviours of both fish and fishing vessels, non-random movement may cause underor overestimation of population size.

The most recent CCAMLR estimates of population size assume that the estimated survival rates of fish and of tags are correct. However, there are potentially large and currently unknowable errors in estimates of the survival of tags, the survival of fish during or as a result of the tagging process and the survival of fish in general. We present a

rather lengthy discussion of these problems, not only because mortality rates are important parameters for both assessments and projections, but also because the lack of acknowledgement of uncertainties in their estimates of these rates by Hanchet *et al.* (2015a).

Take the case of mortality as a result of tagging. The value consistently used by CCAMLR analyses (most recently Mormede et al. (2014a)) was based on mortality for a different species (Patagonian toothfish) in another location, where individuals were observed in a tank on the fishing vessel for 12 h immediately post-tagging. Hanchet et al. (2015a) argue that doubling the mortality observed for 'healthy' fish in this crude half-day experiment (as in CCAMLR's analysis) makes the resulting estimate precautionary. However, the effects of tagging on mortality after the first 12 h are completely unknown, and the observed 12-h mortality in the D. eleginoides study was likely lower than it would have been in the ocean because of the absence of larger predators (other toothfish, seals, toothed whales; Constable 2004; his figure 4) in the experimental tank. In fact, Petrov and Tatarnikov (2010) argue that the tagged individual they recovered in the stomach of a larger AnT was probably consumed shortly after tagging. The fact that long-lasting (6 months) effects on growth are also assumed to occur in the CCAMLR analysis makes it clear that the negative effects of tagging are not confined to the first 12 h. Many studies in behavioural ecology show that organisms experiencing decreased food intake usually increase their level of risk-taking during foraging (e.g. Werner and Anholt 1993; Heithaus et al. 2008), so they should also experience greater mortality throughout that period. There are cases where aquarium studies and/or studies of related species greatly underestimated tagging mortality (e.g. Ebner et al. 2009). Given the variety of potential unobserved mortality effects, total tagging-related mortality for D. mawsoni in the wild could easily exceed that of the healthy subset of the D. eleginoides used in the 12-h tank observations by more than a factor of two. If so, population estimates will be inflated.

Abrams (2014) argued that the natural mortality rate estimates for adult fish in nature by CCAMLR had wide confidence intervals; the resulting range of potential natural mortalities needs to be included in assessing confidence intervals of population estimates and model forecasts. In

response, Hanchet et al. (2015a) inaccurately suggested that Abrams (2014) had claimed that their mortality estimates were based on life-history invariants. Hanchet et al. (2015a) state that their new figure of 13% annual natural mortality is precautionary because this value is slightly below the mean of values produced by their three different mortality estimation methods. This again ignores the wide confidence intervals associated with all three estimation methods. Mortality is assumed to be independent of age and size by Hanchet et al. (2015a), but this is generally not the case for long-lived animals (Finch 1990). Hoenig's (1983) method gives the lowest mortality rates (11-12%) of the three methods Mormede et al. (2014a) examine. However, it is based entirely on the minimum age of the oldest 1% of the population, a parameter likely to be decreased by senescence, inflating the mortality estimate for the majority of the adult life span. Estimates based on this method are also expected to have very wide confidence intervals, as with all extreme value statistics based on limited sample sizes. However, no such intervals have been reported, and all three methods used have wide uncertainties. Wide confidence intervals are acknowledged in CCAMLR analyses of mortality estimates for D. eleginoides (Candy et al. 2011), but not for AnT.

Can management respond rapidly to unexpected population declines?

Assume for the sake of argument that the dynamic model currently used by CCAMLR is accurate for the parts of the life cycle that are observed. Does the type of data currently being obtained ensure that low population sizes will be avoided? Hanchet et al. (2015a) state that the 'adaptive feedback nature' of current management ensures the safety of the AnT stock. 'Adaptive feedback' is the idea that harvest amounts will be reduced (by some as yet unspecified amount) when the stock is estimated to be 'close' (by an unspecified amount) to its target 50% reduction of SSB. Hanchet et al. (2015a, p. 333) assert that their critics have all assumed that no adjustment of the harvest rate will occur at any population size until the limit is reached, when in fact none of the papers critical of CCAMLR management that were cited by Hanchet et al. (2015a) have made such an assumption (see Blight et al. 2010; Jacquet et al. 2010; Ainley et al. 2013; Ainley and

Pauly 2014; Abrams 2014). However, adjustment must occur rapidly enough and to a sufficient extent to prevent unwanted changes in population size. Hanchet *et al.* (2015a) claim that CCAMLR rules ensure meeting their objectives, but do not present or refer to any document where these rules may be found. Several lines of evidence argue against the existence of an adequate procedure.

First, consider the empirical record on feedback; has management actually responded adaptively as new information has become available? The total allowable catch has not been adjusted significantly since the 2003-2004 season, and the publicly available record does not include any consideration of reductions in those quotas up to this time. However, since then, the estimated age of female maturity has been raised from 8 to 17 years, the length for female maturity has been raised from 100 to 141 cm, the estimated SSB is now estimated by CCAMLR (CCAMLR, 2013) to have declined by 25% and the decrease may be significantly greater. In addition, the estimated natural mortality has been decreased from a range of 0.15-0.20 to a uniform 0.13 [compare CCAMLR (2004) with CCAMLR (2013, 2014b) and Mormede et al. (2014a)], and there has been a major shift in the size-structure of the catch over the past decade (fig. 1 of CCAMLR 2013; D.B. Siniff and D.G. Ainley, unpub.). None of these changes has produced a significant alteration of the annual quota.

Could management adapt quickly enough to avoid unwanted population declines? The lack of knowledge of early life stages means that adverse changes in demographic parameters in adult reproduction and early juvenile stage survival or growth could not be detected until many years after the changes took place. Even shifts in adult mortality rates would have to be large in magnitude and occur over a sustained period to be detected. For instance, what would occur if production of eggs or larvae or survival of young fish during their first year declined greatly, either as an indirect result of fishing (e.g. smaller adults) or because of unrelated environmental change (e.g. the ongoing altered circulation patterns documented by Comiso et al. (2011))? The inability to catch fish near the estimated time of spawning or to census young fish would prevent quick detection of such events. Hanchet et al. (2015a) note that, starting in 2012, annual surveys attempted

to assess numbers of smaller, pre-recruit individuals over the inner Ross Sea shelf, where this stage predominates. However, reported catches over the first three years contain almost no fish <60 cm in length (Mormede et al. 2014c; fig. 12); this corresponds to a minimum age of 5-6 years old. These catches have modal lengths only 10 cm (10%) less than that of the 2013 fisheries catch in area 88.1 (CCAMLR 2013). This means absolutely no population estimates for fish aged <6 year and unreliable estimates at least up to age 8 and perhaps up to 10. It does not seem consistent with the claim in Hanchet et al. (2015a, p. 337) that, '...the present monitoring includes small toothfish (giving a direct indicator of recruitment success)'. Furthermore, because the survey of 'pre-recruit' fish uses only a single vessel, spatial coverage is limited, leading to further uncertainties. The catches had virtually identical size distributions each year of the survey (Mormede et al. 2014c), so it appears that either no different strategy to capture truly small fish has been tried, or the attempts have been unsuccessful.

If we use the same growth and survival rates reported in Mormede et al. (2014a, p. 42), we can calculate the drop in adult female biomass (SSB) that will occur starting 17 years after a sustained failure of reproduction (or first year survival). The event might be detected in the sixth year when the first recruits would have reached a catchable size, but it would probably require several additional years before the scarcity of small individuals could not be dismissed as a temporary drop. Assume very low recruitment began in 2005; it would probably just have been acknowledged in 2015. Under an extremely optimistic scenario, fishing would be halted, spawning grounds would be located, and a way to restore spawning/larval survival discovered by 2017. The next 5 years, 2017-2022, would have normal female recruitment due to young born 2000-2005, but would be followed in 2022-2034 by 12 years of no recruits to the adult female population. Using CCAMLR (2013) to project SSB until 2017, with 5 years of recovery afterwards, the 2022 SSB would likely be close to the 2013 value of 75% of B₀. During the 12-year period of no recruits that begins in 2022, the adult female SSB would decline to 24.3% of its 2022 value or 18.2% of B₀. It is hard to see how such an outcome can be described as the product of precautionary management given the strictures in the CCAMLR Articles.

The exact scenario described above is unlikely, but the potential for comparable decreases in SSB because of spawning or recruitment problems is not. The assumption of complete reproductive failure in our scenario decreases the minimum population size, but the assumption that the problem begins as early as 2005 increases that minimum. In fact, because significant fishing has occurred for less than the female maturation time, the shift in adult size distribution and/or failure to correctly identify the SRR could decrease the number of recruits below CCAMLR's expectations by 1/2 or more. If the putative reproductive failure discussed above started after the adult population had declined to its target 50% biomass, the minimum biomass reached after a 12-year reproductive failure would be lower; even an 8-year failure would be expected to reduce the population below 15% of B₀, conservatively assuming fishing mortality increases annual mortality from 13% to 17%.

Unexpectedly large and persistent reductions in recruitment are quite possible, given that the combined effects of reduced abundance and smaller size of adults, ongoing environmental changes, and human activities on spawning and larval survival are largely unknown. Effects of rapidly changing global climate and ocean chemistry and circulation on early AnT life stages are a particular concern (Cheung et al. 2009, 2010). In discussing the biology of early life stages, Constable et al. (2014, p. 3015) warned that, 'toothfish may also be vulnerable to a changing environment'. Spawning is assumed to be restricted to northern seamounts (Hanchet et al. 2008, 2015b; Ashford et al. 2012). Koslow et al. (2000) had earlier noted the particularly high risk of collapse of exploited deepwater species in part because of their tendency to reproduce on seamounts, which represent limited and fragile habitat. The shallower environment of these sites is likely to be more susceptible to the effects of climate change (cf. Cheung et al. 2009, 2010; Pitcher et al. 2010). Egg and larval travel from the sea mounts and vicinity to the Ross Sea shelf is another issue and is purportedly done passively in the Ross Gyre (Hanchet et al. 2008; Ashford et al. 2012). However, salinity is undergoing rapid change in the Gyre as coastal ice shelves melt (Jacobs 2006; Jacobs and Giulivi 2010), thus potentially affecting the buoyancy of eggs, larvae and juveniles. In addition, the speed of the Gyre is increasing; with occasional slowing related to El Nino climate patterns, its flow rate has almost doubled during the last two decades owing to larger scale 'global climate change' (Comiso *et al.* 2011). This suggests that environmentally caused alterations in recruitment are not very low probability events. Elsewhere in the Southern Ocean, where unprecedented environmental change is also underway, depleted stocks of two demersal fish have failed to recover since becoming economically unviable in the early 1980s and then closed to fishing by CCAMLR in 1990 (Marschoff *et al.* 2012).

The differential depletion of large individuals by the fishery could prevent compensation in per capita reproduction that might otherwise occur. The proportional investment in reproduction increases with size in fish (e.g. Longhurst 2010) and fishery-caused mortality will decrease the proportion of larger more fecund individuals. Depletion of larger individuals could also lead to poorer survival rates of larvae due to maternal effects (Hixon et al. 2014). CCAMLR (2013) acknowledged the reduced relative abundance of large fish in the main fishing grounds of the Ross Sea slope. Hanchet et al.'s (2015a, p. 337) statement that, 'This information [on early life-history stages] would have little impact on estimates of...current stock status...' is contradicted by the above examples (if 'status' includes the projections for the near future).

Is Antarctic toothfish harvest precautionary with respect to ecosystem effects?

Uncertainties in predictions are magnified when considering the indirect effects of harvesting AnT on the dynamics of other species (Convention Article II(3b,c)). Here, all of the ecosystem analyses cited in Hanchet et al. (2015a) rely on a nondynamic model (Pinkerton et al. 2010; Pinkerton and Bradford-Grieve 2014) that describes energy flows among broadly defined elements of the food web. This, in turn, is based on a method of adjusting highly uncertain estimates of diets so that they imply mass balance (Ecopath with Ecosim; Christensen and Walters 2004). 'Balancing' the estimates about energy flows does nothing to reduce the uncertainty about the magnitudes of those flows. Pinkerton and Bradford-Grieve (2014) use the Ecopath-adjusted flow estimates to calculate the effects of an infinitesimal change in abundance on the flow of energy between species. Without a dynamic model, these cannot be used to estimate

the impact of large changes in the abundance of any species (here, AnT changing by 50%). It is well-known that extrapolation from infinitesimal changes is not valid even in 'linear' (i.e. Lotka-Volterra) systems because ecosystem components may invade or go extinct based on the perturbation (Abrams 2001). It is even more unreliable for systems with highly nonlinear per capita growth rates, which is likely to be the vast majority of systems (Abrams 2001, 2009a, 2010). Use of such a model is made more questionable by the seasonal shifts in distribution and behaviour that has been observed in bird and mammal species that represent potential predators and/or competitors of AnT (e.g. Ainley et al. 2015a), as well as the uncoupled nature of upper and lower trophic levels (e.g. Ainley et al. 2015b). The poorly known shift in AnT diet with developmental changes in buoyancy (Near et al. 2003) is another complicating factor in this system.

Because AnT are the only abundant large predatory fish in the Ross Sea ecosystem and have a generalist diet, they have the potential to impose a large change in the structure of rest of the fish community, as well as some invertebrates at lower trophic levels (see also Gon and Heemstra 1990; Kock 1992; Eastman 1993). This is particularly important in a system where abundant upper trophic level species are competing for the same, limited prey (Ainley *et al.* 2015b). Depletion of large predatory fish elsewhere has had such community-level effects (Myers and Worm 2003; Frank *et al.* 2005).

In considering the 50% of baseline target from the ecosystem perspective, it should be noted that Constable et al. (2000) argued for a lower biomass limit of 75% of baseline for the Antarctic krill harvest, and this is the policy that CCAMLR adopted. The justification was that 50% was a standard limit point in analyses using single-species models, but krill was the food source for many other species, so ecosystem considerations required that the limiting abundance of krill be higher [again, note CCAMLR Article II(3)]. Constable et al. (2000) felt that a supposed lack of predation on toothfish justified the target abundance of 50%, which was standard for single-species models. However, predation by mammals on toothfish had already been documented and has subsequently been shown repeatedly (Yukhov 1971; Ainley and Siniff 2009 and references therein; Ainley and Ballard 2012; Torres et al. 2013: Eisert et al. 2013: see Constable 2004, his figure 4). Thus, the logic applied to krill also argues for a precautionary target AnT population level above $B_0/2$.

If predation on toothfish is indeed insignificant, this could well imply that AnT occupies the role of a keystone top predator (Eastman 1993). General analyses of harvesting in simple food web models (e.g. Matsuda and Abrams 2006) show that harvesting such species frequently causes extinctions at lower trophic levels, and top predators are known for their positive effects on diversity at lower levels in many other ecosystems (Estes et al. 2011). We do not know the Ross Sea food web well enough to justify the belief that a 50% reduction in the AnT population is safe for lower trophic level species. Currently, CCAMLR has no Ecosystem Monitoring Program in place to measure the ecosystem effects of the toothfish fisheries it manages; this again contrasts with the Antarctic krill fishery (www.ccamlr.org/en/science/ccamlrecosystem-monitoring-program-cemp, 15 December 2015).

Is current management sufficiently impartial?

While there are always unknowns in fisheries science, an essential element of a precautionary approach is to recognize that these produce a range of plausible models. If a significant fraction of plausible models lead to unacceptable outcomes under a particular policy, a precautionary approach would be to adopt a different policy. Because the plausible range of models has not been explored for AnT, the advice of Hanchet *et al.* (2015a, p. 339) seems appropriate: 'when key information is inadequate, exploitation rates are reduced to ensure that the precautionary approach is followed'.

In cases with high levels of uncertainty, history often provides a better guide to action than do quantitative analyses based on insufficient data. Ainley and Pauly (2014) historical review of fisheries in the coastal Antarctic documents the many previous instances of over-fishing in this ecosystem (see also Gon and Heemstra 1990; Kock 1992; Ainley and Blight 2009); this history argues for a very conservative interpretation of 'precaution', as does the very slow recovery of other, previously fished Antarctic benthic species (Marschoff *et al.* 2012). Even if unknowns were fewer, as was the case for Atlantic cod, collapse of AnT or other species in the system remain distinct possibilities.

The CAMLR Convention calls for decisions to be based on the best science available (Article IX(f)). Has this been the case for the AnT fishery? As noted in the first half of this article, science in poorly understood fields requires consideration of a range of approaches, preferably by a range of investigators. The concern that values that weight profits over precaution have had too large an influence in this case is bolstered by the source of most of the studies used for stock assessment and population modelling. The large majority of these studies have been carried out following the initiation of the AnT fishery by scientists employed by a government-related agency, New National Institute of Water and Atmosphere (N.I.W.A.). New Zealand has been and still is one of the largest harvesters of AnT (Table 2 of CCAMLR 2013). N.I.W.A. has felt the need to defend the current CCAMLR policies (N.I.W.A. annual report, 2015, p. 75; https://www.niwa.co.nz/sites/niwa.co.nz/files/NIW12101 AR%2020 14-15_16F%20LR.pdf, 8 December 2015). In addition, the N.I.W.A. website displays a video of S. Hanchet claiming '[the fishery]...is probably one of the best managed in the world'. (21 Feb. 2012: https://www.niwa.co.nz/videos/currentand-future-management-of-the-toothfish-fishery). Such claims make it more difficult to change positions in the face of contrary data. Even among initially impartial scientists, there is a reluctance to reverse positions on a controversial issue once a stance has been taken. This illustrates the need for Ludwig et al.'s (1993, p. 36) call to, 'Include human motivation and responses as part of the system to be studied and managed'.

What should be done?

Our example of the Ross Sea region AnT is certainly not among the most over-exploited fish in the world. There are many other fish stocks where the label of 'insufficient precaution' applies (Safina et al. 2005; Rosenberg et al. 2006; Neubauer et al. 2013). Determining the extent to which our five criteria are satisfied should aid in determining what future policy changes are required to restore these populations. Wider recognition of the high levels of uncertainty characterizing most fisheries predictions should be helpful in designing future management protocols.

For AnT, it would clearly be more precautionary to significantly reduce the annual take. Closure of

the fishery until the dynamics of the major components of the ecosystem are better understood should also be considered, in conjunction with an expanded field research programme. If fishing continues, it would be desirable to decrease the annual quota and increase the target spawning stock biomass. This could be accomplished using the same proportional target as in the CCAMLR krill fishery, that is 75% of Bo. This was the 2013 estimate of SSB for Area 88 AnT, implying immediate reductions in the allowable catch. It is worth noting that N.I.W.A. now acknowledges that killer whales and Weddell seals prey on AnT (https:// www.niwa.co.nz/sites/niwa.co.nz/files/NIW12101 _AR%202014-15_16F%20LR.pdf, p. 75), showing an emerging consensus on the importance of AnT as prey of marine mammals in the Antarctic ecosystem. The logic used in Constable et al. (2000) would then argue for a limit point for AnT >B₀/2. Whatever new target is adopted, future research should involve understanding spawning and transport of larvae and very small fish in a dramatically changing flow system. It should also include collecting a multiyear record of population size of young fish and associated environmental variables and continuing and improving population estimation of larger fish. These and other projects should seek involvement by a wider range of scientists to obtain a more complete understanding of the potential population and ecosystem consequences of harvesting. This research should lead to the development of an Ecosystem Monitoring Programme.

Over the years, CCAMLR has instituted a number of desirable policies and protocols related to conservation. These include (www.ccamlr.org): no directed finfish fishing anywhere in FAO Area 48.1, owing to depleted stocks [Conservation Measure (CM) 32-02]; no longlines or bottom trawling at depths <550 m to protect benthic invertebrates (CM 22-08); prohibition on all take of sharks (CM 32-18); and significantly precautionary harvest of krill (various CMs and an Ecosystem Monitoring Programme). Nevertheless, in many respects, the level of precaution in regulating the Ross Sea AnT fishery does not appear to be substantively different from many purely extractive fisheries on better known species in less sensitive and less protected environments. The lack of knowledge that poses a problem for management is also a problem for longer term prediction of the size of the AnT population. We have concentrated on potential risks of population decline here, as these risks are what the precautionary approach is designed to avoid.

Careful consideration of the questions we outline here can help to improve the application of a precautionary and ecosystem-based approach to sustainably manage not only AnT, but also exploited fish populations elsewhere in the world. The fact that a more precautionary approach has not been followed for AnT so far should itself serve as a cautionary message to those who feel that fisheries elsewhere are safe from future over-exploitation.

Acknowledgements

We thank R. Hofman, M. Burgess, H. Giacomini, J. Hutchings and C. Clark and the anonymous reviewers for comments on earlier drafts. PAA was supported by a Discovery Grant from NSERC Canada; DGA's efforts were supported by NSF grant Ant-0944411. Jennifer L. Jacquet was supported by an Alfred P. Sloan Research Fellowship.

References

Abrams, P.A. (2001) Describing and quantifying interspecific interactions; A commentary on recent approaches. Oikos 94, 209–218.

Abrams, P.A. (2009a) Determining the functional form of density dependence; deductive approaches for consumer-resource systems with a single resource. American Naturalist 174, 321–330.

Abrams, P.A. (2009b) The implications of using multiple resources for consumer density dependence. Evolutionary Ecology Research 11, 517–540.

Abrams, P.A. (2009c) When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. *Ecology Let*ters 12. 462–474.

Abrams, P.A. (2010) Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology* **24**, 7–17.

Abrams, P.A. (2011) Simple life history omnivory: responses to enrichment and harvesting in systems with intraguild predation. *American Naturalist* **178**, 305–319.

Abrams, P.A. (2014) How precautionary is the policy governing the Ross Sea Antarctic toothfish (*Dissostichus mawsoni*) fishery? *Antarctic Science* **26**, 3–13.

Abrams, P.A., Ruokolainen, L.R., Shuter, B.J. and McCann, K.S. (2012) Harvesting creates ecological traps; consequences of invisible mortality risks in predator-prey metacommunities. *Ecology* **93**, 281–293. Agnew, D.J., Gutierrez, N.L., Stern-Pirlot, A., Smith, A.D.M., Zimmermann, C. and Sainsbury, K. (2013)

- Rebuttal to Froese and Proelss "Evaluation and legal assessment of certified seafood. *Marine Policy* **38**, 551–553.
- Ainley, D.G. and Ballard, G. (2012) Trophic Interactions and the decrease in killer whale (*Orcinus orca*) prevalence with reduced availability of large fish in the southern Ross Sea. *Aquatic Mammals* **38**, 153–160.
- Ainley, D.G. and Blight, L.K. (2009) Ecological repercussions of historical fish extraction from the Southern Ocean. *Fish and Fisheries* **10**, 13–38.
- Ainley, D.G. and Pauly, D. (2014) Fishing down the food web of the Antarctic continental shelf and slope. *Polar Record* 50, 92–107.
- Ainley, D.G. and Siniff, D.B. (2009) The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. Antarctic Science 21, 317–327.
- Ainley, D.G., Nur, N., Eastman, J.T. et al. (2013) Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972-2011. Fish and Fisheries 14, 343–363.
- Ainley, D.G., LaRue, M.A., Stirling, I., Stammerjohn, S. and Siniff, D.B. (2015a) An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. *Marine Mammal Science* 31, 1338–1361.
- Ainley, D.G., Ballard, G., Jones, R.M. et al. (2015b) Trophic cascades in the western Ross Sea, Antarctica: revisited. Marine Ecology Progress Series 534, 1–16.
- Ashford, J., Dinniman, M., Brooks, C. et al. (2012) Does large-scale ocean circulation structure life history connectivity in Antarctic toothfish (Dissostichus mawsoni)? Canadian Journal of Fisheries and Aquatic Science 69, 1903–1919.
- Beddington, J.R. and Cooke, J.G. (1983) The potential yield of fish stocks. FAO FisheriesTechnical Paper 242, 47 pp.
- Beddington, J.R., Agnew, D.J. and Clark, C.W. (2007) Current problems in the management of marine fisheries. *Science* 316, 1713–1716.
- Belgrano, A. and Fowler, C.W. (2013) How fisheries affect evolution. *Science* **342**, 1176–1177.
- Blight, L.K., Ainley, D.G., Ackley, S.F. et al. (2010) Fishing for data in the Ross Sea. Science 330, 1316–1316.
- Candy, S.G., Welsford, D.C., Lamb, T., Verdouw, J.J. and Hutchins, J.J. (2011) Estimation of natural mortality for the Patagonian toothfish at Heard and McDonald Islands using catch-at-age and aged mark-recapture data from the main trawl ground. CCAMLR Science 18, 29–45.
- CCAMLR (2004) Report of the Working Group on Fish Stock Assessment (11–22 October 2004) Hobart, TAS Australia: Commission for the Conservation of Antarctic Marine Living Resources.
- CCAMLR (2011) Fishery Report 2011, Appendix R: Exploratory fishery for *Dissostichus* spp. in Subareas 88.1 and 88.2. Hobart, TAS Australia: Commission for the Conservation of Antarctic Marine Living Resources.

- CCAMLR (2012) Report of the working group on fish stock assessment. Document WG-FSA-12. Hobart, TAS Australia: Commission for the Conservation of Antarctic Marine Living Resources.
- CCAMLR (2013) Fishery Report 2013: Exploratory fishery for *Dissostichus* spp. in Subareas 88.1 and 88.2. Hobart, TAS Australia: Commission for the Conservation of Antarctic Marine Living Resources.
- CCAMLR (2014a) Report of the working group on fish stock assessment. document WG-FSA-14. Hobart TAS: Commission for the Conservation of Antarctic Marine Living Resources.
- CCAMLR (2014b) Fishery report 2014: Exploratory fishery for *Dissostichus* spp. in Subareas 88.1 and 88.2.
 Hobart TAS: Commission for the Conservation of Antarctic Marine Living Resources.
- CCAMLR (2014c) Report of the Thirty-third Meeting of the Commission. Hobart TAS: Commission for the Conservation of Antarctic Marine Living Resources.
- Cheung, W.W.L., Lam, V., Sarmiento, J., Kearney, K., Watson, R. and Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries 10, 235–251.
- Cheung, W.W.L., Lam, V., Sarmiento, J., Kearney, K., Watson, R. and Pauly, D. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Global Change Biology. 16, 24–35.
- Christian, C., Ainley, D., Bailey, M. et al. (2013a) Not "the best environmental choice in seafood": a response to Gutierrez and Agnew (2013). Biological Conservation 165, 214–215.
- Christian, C., Ainley, D., Bailey, M. et al. (2013b) A review of formal objections to Marine Stewardship Council fisheries certifications. Biological Conservation 161, 10–17.
- Christensen, V. and Walters, C.J. (2004) Ecopath with Ecosim: methods capabilities and limitations. *Ecological Modelling* 172, 109–139.
- Clark, C.W. (2007) The Worldwide Crisis in Fisheries. Cambridge University Press, Cambridge.
- Clark, C.W. (2010) Challenges in Marine Capture Fisheries. In: Handbook of Marine Fisheries; Conservation and Management. (eds R.Q. Grafton, R. Hilborn, D. Squires et al.). Oxford University Press, New York, NY, pp. 638–647.
- Clark, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003) North Sea cod and climate change – modelling the effects of temperature on population dynamics. Global Change Biology 9, 1669–1680.
- Comiso, J.C., Kwok, R., Martin, S. and Gordon, A.L. (2011) Variability and trends in sea ice extent and ice production in the Ross Sea. *Journal of Geophysical Research* 116, C04021.
- Constable, A.J. (2004) Managing fisheries effects on marine food webs in Antarctica: trade-offs among harvest

- strategies, monitoring, and assessment in achieving conservation objectives. *Bulletin of Marine Science* **74**, 583–605.
- Constable, A.J. (2011) Lessons from CCAMLR on the implementation of the ecosystem approach to managing fisheries. Fish and Fisheries 12, 138–151.
- Constable, A.J., de la Mare, W.K., Agnew, D.J., Everson, I. and Miller, D. (2000) Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of Marine Science 57, 778–791.
- Constable, A.J., Melbourne-Thomas, J., Corney, S.P. et al. (2014) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. Global Change Biology 20, 3004–3025.
- Croxall, J.P. and Nicol, S. (2004) Management of Southern Ocean fisheries: global forces and future sustainability. *Antarctic Science* **16**, 569–584.
- Darimont, C.T., Fox, C.H., Bryan, H.M. and Reimchen, T.E. (2015) The unique ecology of human predators. *Science* 349, 858–860.
- Daskalov, G.M., Grishin, A.N., Rodionov, S. and Mihneva, V. (2007) Trophic cascades triggered by over-fishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Sciences (USA) 104, 10518–10523.
- Dayton, P. (1998) Reversal of the burden of proof in fisheries management. *Science* 279, 821–822.
- DeRoos, A. and Persson, L. (2013) *Population and community ecology of ontogenetic development*. Princeton University Press, Princeton.
- Dulvy, N.K., Sadovy, Y. and Reynolds, J.D. (2003) Extinction vulnerability in marine populations. Fish and Fisheries 4, 25–64.
- Dunlop, E.S., Eikeset, A.M. and Stenseth, N.C. (2015) From genes to populations: how fisheries-induced evolution alters stock productivity. *Ecological Applications*. 25, 1860–1868.
- Dunn, A., Horn, P.L. and Hanchet, S.M. (2006) Revised estimates of the biological parameters for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea. Document WG-FSA-SAM-06/8. Hobart, TAS: Commission for the Conservation of Antarctic Marine Living Resources.
- Eastman, J.T. (1993) Antarctic Fish Biology: Evolution in a Unique Environment. Academic Press, San Diego.
- Ebner, B.C., Lintermans, M., Jekabsons, M., Dunford, M. and Andrews, W. (2009) A cautionary tale: surrogates for radio-tagging practice do not always simulate the responses of closely related species. *Marine and Freshwater Research* 60, 371–378.
- Eisert, R., Pinkerton, M.H., Newsome, S.D. and Oftedal, O.T. (2013) A critical re-examination of the evidence for a possible dependence of Weddell seals (*Leptony-chotes weddellii*) on Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. Document

- SCCAMLR-WG-EMM-13.28. Hobart, TAS, Australia: Commission for the Conservation of Antarctic Marine Living Resources.
- Engen, S., Lande, R. and Saether, B.-E. (2014) Evolutionary consequences of nonselective harvesting in density-dependent populations. *American Naturalist* 184, 714–726.
- Estes, J.A., Terborgh, J., Brashaers, J.S. et al. (2011) Trophic downgrading of planet earth. Science 333, 301–306.
- Finch, C.E. (1990) Longevity, Senescence, and the Genome. University of Chicago Press, Chicago.
- Frank, K.T., Petrie, B., Choi, J.S. and Leggett, W.C. (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623.
- Froese, R. and Proelss, H. (2010) Rebuilding fish stocks no later than 2015: will Europe meet the deadline? *Fish and Fisheries* **11**, 194–202.
- Froese, R. and Proelss, H. (2012) Evaluation and legal assessment of certified seafood. *Marine Policy* **36**, 1284–1289.
- Froese, R. and Proelss, H. (2013) Is a stock overfished if it is depleted by overfishing? A response to the rebuttal of Agnew et al. to Froese and Proelss "Evaluation and legal assessment of certified seafood" *Marine Policy* **38**, 548–550.
- Fulton, E.A., Link, J.S., Kaplan, I.C. et al. (2011) Lessons in modeling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries 12, 171–188.
- Gon, O. and Heemstra, P.C. (1990) Fishes of the SouthernOcean. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. 462 pp.
- Grafton, R.Q., Kompas, T. and Hilborn, R. (2007) Economics of overexploitation revisited. Science 318, 1601
- Grafton, R.Q., Hilborn, R., Ridgeway, L. et al. (2008) Positioning fisheries in a changing world. Marine Policy 32, 630–634.
- Halpern, B.S., Walbridge, S., Selkoe, K.A. et al. (2008) A global map of human impact on marine ecosystems. Science 319, 948–952.
- Hanchet, S.M., Rickard, G.J., Fenaughty, J.M., Dunn, A. and Williams, M.J.H. (2008) A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. CCAMLR Science 15, 35–53.
- Hanchet, S., Sainsbury, K., Butterworth, D. et al. (2015a) CCAMLR's precautionary approach to management focusing on Ross Sea toothfish fishery. Antarctic Science 27, 333–340.
- Hanchet, S., Dunn, A., Parker, S., Horn, P., Stevens, D. and Mormede, S. (2015b) The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region. *Hydrobiologia* 761, 397–414.
- Harwood, J. and Stokes, K. (2003) Coping with uncertainty in ecological advice: lessons from fisheries. Trends in Ecology and Evolution 18, 617–622.

- Heithaus, M.R., Frid, A., Wirsing, A.J. and Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23, 202–210.
- Hilborn, R. (2002) The dark side of reference points. *Bulletin of Marine Science* **70**, 403–408.
- Hilborn, R. (2010) Pretty good yield and exploited fisheries. Marine Policy 34, 193–196.
- Hilborn, R., Maguire, J.-J., Parma, A.M. and Rosenberg, A.A. (2001) The precautionary approach and risk management: can they increase the probability of successes in fisheries management? *Canadian Journal of Fisheries and Aquatic Sciences.* 58, 99–107.
- Hilborn, R., Hively, D.J., Jensen, O.P. and Branch, T.A. (2014) The dynamics of fish populations at low abundance and prospects for rebuilding and recovery. ICES Journal of Marine Science 71, 2141–2151.
- Hill, S.L., Watters, G.M., Punt, A.E. *et al.* (2007) Model uncertainty in the ecosystem approach to fisheries. *Fish and Fisheries* **8**, 315–336.
- Hixon, M.A., Johnson, D.W. and Sogard, S.M. (2014) BOFFFFs: on the importance of conserving old-growth age structure in fisheries populations. ICES Journal of Marine Science 71, 2171–2185.
- Hjermann, D.Ø., Bogstad, B., Eikeset, A.M., Otterson, G., Gjøsæter, H. and Stenseth, N.J. (2007) Food web dynamics affect Northeast Arctic cod recruitment. Proceedings of the Royal Society B 274, 661–669.
- Hoenig, J.M. (1983) Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 81, 899– 903
- Hsieh, C.-H., Reiss, C.S., Hunter, J.R., Beddington, J., May, R.M. and Sugihara, G. (2006) Fishing elevates variability in the abundance of exploited species. *Nat-ure* 443, 859–862.
- Hurtado-Ferro, F., Szuwalski, C.S., Valero, J.L. *et al.* (2015) Looking in the rear-view mirror: bias and retrospective patterns in integrated age-structured stock assessment models. *ICES Journal of Marine Science* **72**, 99–110.
- Hutchings, J.A. (2000) Collapse and recovery of marine fishes. *Nature* **406**, 882–885.
- Hutchings, J.A. (2014) Renaissance of a caveat: Allee effects in marine fish. ICES Journal of Marine Science 71, 2152–2157.
- Hutchings, J.A. (2015) Thresholds for impaired species recovery. Proceedings of the Royal Society B 282, 20150654.
- Hutchings, J.A. and Myers, R.A. (1994) What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2126–2146.
- Hutchings, J.A. and Reynolds, J.D. (2004) Marine fish population collapses: Consequences for recovery and extinction risk. *BioScience* 54, 297–309.

- Hutchings, J.A., Walters, C.J. and Haedrich, R.L. (1997) Is scientific inquiry incompatible with government information control? *Canadian Journal of Fisheries and Aquatic Sciences* 54, 1198–1210.
- Jacobs, S. (2006) Observations of change in the Southern Ocean. Philosophical Transactions of the Royal Society A. 364, 1657–1681.
- Jacobs, S.S. and Giulivi, C. (2010) Large multidecadal salinity trends near the Pacific-Antarctic continental margin. *Journal of Climate* 17, 4508–4524.
- Jacquet, J., Pauly, D., Ainley, D., Holt, S. and Jackson, J. (2010) Seafood stewardship in crisis. *Nature* 476, 28–29
- Jorgensen, C., Enberg, K., Dunlop, E.S. et al. (2007) Managing evolving fish stocks. Science 318, 1247– 1248.
- Kock, K.-H. (1992) Antarctic Fish and Fisheries. Cambridge University Press, Cambridge and New York. 359 pp.
- Kock, K.-H. (2007) Antarctic Marine Living Resources exploitation and its management in the Southern Ocean. Antarctic Science 19, 231–238.
- Koen-Alonzo, M. and Yodzis, P. (2005) Multispecies modeling of some components of the marine community of northern and central Patagonia, Argentina. Canadian Journal of Fisheries and Aquatic Sciences 62, 1490–1512.
- Koslow, J.A., Boehlert, G.W., Gordon, J.D.M., Haedrich, R.L., Lorance, P. and Parin, N. (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science* 57, 548– 557.
- Kuparinen, A., Stenseth, N.C. and Hutchings, J.A. (2014) Fundamental population-productivity relationships can be modified through density-dependent feedbacks of life-history evolution. Evolutionary Applications 7, 1218–1225.
- Lande, R., Saether, B.E. and Engen, S. (1995) Optimal harvesting of fluctuating populations with a risk of extinction. *American Naturalist* 145, 728–745.
- Lande, R., Saether, B.E. and Engen, S. (1997) Threshold harvesting for sustainability of fluctuating resources. *Ecology* 78, 1341–1350.
- Lauck, T., Clark, C.W., Mangel, M. and Monro, G.R. (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8, S72–S78.
- Laugen, A.T., Engelhard, G.H., Whitlock, R. et al. (2014) Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. Fish and Fisheries 15, 65–96.
- Lawton, J.H. (1999) Are there general laws in ecology? Oikos 84, 177–192.
- Longhurst, A. (2010) Mismanagement of marine fisheries. Cambridge University Press, Cambridge.

- Ludwig, D. (1998) Management of stocks that may collapse. Oikos 83, 397–402.
- Ludwig, D. (2002) A quantitative precautionary approach. Bulletin of Marine Science 70, 485–497.
- Ludwig, D., Hilborn, R. and Walters, C. (1993) Uncertainty, resource exploitation, and conservation. Science 260, 17–18
- MacCall, A.D. (2002) Fishery management and stock rebuilding prospects under conditions of low frequency variability and species interactions. *Bulletin of Marine Science* **70**, 613–628.
- MacCall, A.D., Hill, K.T., Crone, P. and Emmett, R. (2012) Weak evidence of sardine collapse. Proceedings of the National Academy of Sciences 109, E1131.
- Mace, P.M. (2001) A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish and Fisheries 2, 2–32.
- Mangel, M., MacCall, A.D., Brodziak, J. et al. (2013) A perspective on steepness, reference points, and stock assessment. Canadian Journal of Fisheries and Aquatic Sciences 70, 930–940.
- Marschoff, E.R., Barrera-Oro, E.R., Alescio, N.S. and Ainley, D.G. (2012) Slow recovery of previously depleted demersal fish at the South Shetland Islands, 1983–2010. Fisheries Research 125(126), 206–213.
- Matsuda, H. and Abrams, P.A. (2006) Maximal yields from multi-species fisheries systems: rules for systems with multiple trophic levels. *Ecological Applications*. 16, 225–237.
- Matsuda, H. and Abrams, P.A. (2013) Is feedback control effective for ecosystem-based fisheries management? *Journal of Theoretical Biology* 339, 122–128.
- May, R.M. (2004) Uses and abuses of mathematics in biology. *Science* **303**, 790–793.
- Millner, A., Dietz, S. and Heal, G. (2013) Scientific ambiguity and climate policy. Environmental Resource Economics 55, 21–46.
- Mormede, S., Dunn, A. and Hanchet, S.M. (2014a) A stock assessment model of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region incorporating multi-year mark-recapture data. *CCAMLR Science* **21**, 39–62.
- Mormede, S., Dunn, A. and Hanchet, S.M. (2014b) Spatially explicit population dynamics models for Antarctic toothfish in the Ross Sea region. CCAMLR Science 21, 19–37.
- Mormede, S., Parker, S.J., Hanchet, S.M., Dunn, A. and Gregory, S. (2014c) Results of the third CCAMLR sponsored research survey to monitor abundance of subadult Antarctic toothfish in the southern Ross Sea, February 2014 and development of time series. Document WG-FSA-14/51. Hobart TAS, Australia: Commission for the Conservation of Antarctic Marine Living Resources.
- Myers, R.A. and Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.

- Myers, R.A., Bowen, K.G. and Barrowman, N.J. (1999) Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56, 2404–2419.
- Near, T.J., Russo, S.E., Jones, C.D. and Devries, A.L. (2003) Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). *Polar Biology* 26, 124– 128
- Neubauer, P., Jensen, O.P., Hutchings, J.K. and Baum, J.K. (2013) Resilience and recovery of overexploited marine populations. *Science* 340, 347–349.
- O'Brien, K.M. and Crockett, E.L. (2013) The promise and perils of Antarctic fishes. *EMBO Reports* **14**, 17–24.
- O'Riordan, T. and Cameron, J. (1995) *Interpreting the pre-cautionary principle*. Earthscan Publications, London.
- Österblom, H., Sumaila, U.R., Bodin, Ö., Sundberg, J.H. and Press, A.J. (2010) Adapting to Regional Enforcement: fishing Down the Governance Index. *PLoS ONE* **5**(9), e12832.
- Pella, J.J. and Tomlinson, P.K. (1969) A generalized stock production model. Bulletin of the Inter-American Tropical Tuna Commission 13, 419–496.
- Petrov, A.F. and Tatarnikov, V.A. (2010) New data on migrations of Antarctic toothfish *Dissostichus mawsoni* in the Dumont d'Urville Sea in the 2008/2009 season. *Journal of Ichthyology* 50, 140–141.
- Pinkerton, M.H. and Bradford-Grieve, J.M. (2014) Characterizing foodweb structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica. ICES Journal of Marine Science 71, 1542–1553.
- Pinkerton, M.H., Bradford-Grieve, J.M. and Hanchet, S.M. (2010) A balanced model of the food web of the Ross Sea, Antarctica. CCAMLR Science 17, 1–31.
- Pitcher, T.J., Clark, M.R., Morato, T. and Watson, R. (2010) Seamount fisheries: do they have a future? *Oceanography* 23, 134–144.
- Plagányi, E. and Butterworth, D.S. (2004) A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. *African Journal of Mar*ine Science 26, 261–287.
- Plagányi, E.E., Punt, A.E., Hillary, R. et al. (2014) Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish and Fisheries 15, 1–22.
- Punt, A.E. (2006) The FAO precautionary approach after almost 10 years: have we progressed towards implementing simulation-tested feedback-control management systems for fisheries management? Natural Resource Modeling 19, 441–464.
- Quiggin, J. (2010) Zombie Economics: How Dead Ideas Still Walk among Us. Princeton University Press, Princeton, N.J.
- Restrepo, V.R. (ed) (1999) Proceedings of the Fifth National NMFS Stock Assessment Workshop Providing Scientific Advice to Implement the Precautionary

- Approach Under the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum NMFS-F/SPO-40. National Marine Fisheries Service, Washington DC.
- Reynolds, J.D., Dulvy, N.K., Goodwin, N.B. and Hutchings, J. (2005) Biology of extinction risk in marine fishes. Proceedings of the Royal Society, B. 272, 2337–2344.
- Ricard, D., Minto, C., Jensen, O.P. and Baum, J.K. (2012) Examining the knowledge base and status of commercially exploited marine species with the RAM legacy stock assessment database. Fish and Fisheries 13, 380–398
- Richards, L.J. and Maguire, J.-J. (1998) Recent international agreements and the precautionary approach: new directions for fisheries management science. Canadian Journal of Fisheries and Aquatic Sciences 55, 1545–1552
- Rosenberg, A.A. (2002) The precautionary approach in application from a manager's perspective. Bulletin of Marine Science 70, 577–588.
- Rosenberg, A.A., Swasey, J.H. and Bowman, M. (2006) Rebuilding US fisheries: progress and problems. Frontiers in Ecology and the Environment 4, 303–308.
- Roughgarden, J. and Smith, F. (1996) Why fisheries collapse and what to do about it. *Proceedings of the National Academy of Sciences (USA)* **93**, 5078–5083.
- Safina, C., Rosenberg, A.A., Myers, R.A., Quinn, T.J.I.I. and Collie, J.S. (2005) U.S. Ocean fish recovery: staying the course. *Science* 309, 707–708.
- Sainsbury, K.J., Punt, A.E. and Smith, A.D.M. (2000) Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science* 57, 731–741.
- Schnute, J.T. and Richards, L.J. (2001) Use and abuse of fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences.* **58**, 10–17.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J. and Pagel, M. (2005) On the regulation of populations of mammals, birds, fish, and insects. *Science* **309**, 607–610.
- Stammerjohn, S., Massom, R., Rind, D. and Martinson, D. (2012) Regions of rapid sea ice change: an interhemispheric seasonal comparison. *Geophysical Research Letters* 39, L06501.
- Stewart, I.J. and Martell, S.J.D. (2015) Reconciling stock assessment paradigms to better inform fisheries management. ICES Journal of Marine Science 72, 2187– 2196.

- Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A. and Hilborn, R. (2015) Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish* and *Fisheries* 16, 633–648.
- Thorson, J.T., Cope, J.M., Branch, T.A. and Jensen, O.P. (2012) Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 1556–1568.
- Torres, L., Pinkerton, M.H., Pitman, R., Durban, J. and Eisert, R. (2013) To what extent do type C killer whales (*Orcinus orca*) feed on Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica? Document SC-CAMLR-WG-EMM-13.29. Hobart, TAS, Australia: Commission for the Conservation of Antarctic Marine Living Resources.
- VanderZwaag, D.L., Hutchings, J.A., Jennings, S. and Peterman, R.M. (2012) Canada's international and national commitments to sustain marine biodiversity. *Environmental Reviews* 20, 312–352.
- Walters, C.J. and Kitchell, J.F. (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 39–50.
- Walters, C.J. and Martell, S.J.D. (2002) Stock assessment needs for sustainable fisheries management. Bulletin of Marine Science 70, 629–638.
- Weitzman, M.L. (2009) On modeling and interpreting the economics of catastrophic climate change. *The Review of Economics and Statistics* **9**, 1–19.
- Werner, E.E. and Anholt, B.R. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* **142**, 242–272.
- Yeakel, J.D. and Mangel, M. (2015) A generalized perturbation approach for exploring stock recruitment relationships. *Theoretical Ecology* 8, 1–13.
- Yodzis, P. (1988) The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69, 508–515.
- Yukhov, V.L. (1971) The range of Dissostichus mawsoni Norman and some features of its biology. Journal of Ichthyology 11, 8–18.
- Zhou, S., Yin, S., Thorson, J.T., Smith, A.D.M. and Fuller, M. (2012) Linking fishing mortality reference points to life history traits: an empirical study. *Canadian Journal* of Fisheries and Aquatic Sciences 69, 1292–1301.