The ecological and evolutionary effects of harvesting Northeast Arctic cod
- Insights from economics and implications for management

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Dissertation for the degree Philosophiae Doctor (PhD)

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2010

ACKNOWLEDGEMENTS

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In Ecosystem Based Management for Marine Fisheries: An Evolving Perspective (ed. A. Belgrano & C. W. Fowler), Cambridge University Press. Accepted.

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INTRODUCTION

About Northeast Arctic cod

Northeast Arctic cod (NEA cod) is the world largest stock of Atlantic cod (*Gadus morhua*), and an important economic resource with annual recorded catch between 400,000 and 500,000 tonnes. In 2009, the value of the cod fishery was about 3.5 billion NOK and more than 50% of the Atlantic cod sold worldwide comes from the Barents Sea. The NEA cod is distributed in the Barents Sea and along the Norwegian coast (Figure 1). The fish mature at about 6 years of age and then migrate out of the Barents Sea to spawn further south in various locations off the Norwegian west coast. The largest spawning site is located around the Lofoten islands. This spawning cod is caught and referred to as "skrei" in Norwegian. After about 3 months, the mature fish return to their feeding grounds in the Barents Sea.

The cod eggs that are spawned develop into larvae and are advected by the Norwegian Coastal Current northward along the coast into the Barents Sea (Figure 1). The larvae grow up in the Coastal Current, feeding on plankton. When the cod is above the age of 2-3 years, its key prey species is capelin (*Mallotus villosus*). Is has been shown that if the capelin biomass is high, this has a positive effect on the cod population, indicated by increased liver energy, egg production and spawner biomass (Marshall et al. 1999). Capelin is also important for the survival of young cod since cannibalism is an important factor for mortality in the early age classes of cod (Yaragina et al. 2009). Thus, if capelin abundance is low, the 1-2 year old cod are more likely to be eaten by larger cod. However, capelin recruitment is heavily affected by 1-2 year old Norwegian Spring-Spawning (NSS) herring (*Clupea harengus*) which eat capelin larvae (Gjøsæter & Bogstad 1998). If the abundance of young herring is high, there will be a likely decrease in the abundance of capelin 2-3 years later (Hjermann et al. 2007a). Therefore, herring also affect the cod stock. The herring live partly in the Barents Sea (until the age of 3) and partly in the Norwegian Sea. Recruitment (i.e., larval mortality) of the herring, a key species in this system, is extremely variable from year to year, in part linked to variations in sea climate (Fiksen & Slotte 2002).

Climate may also affect the distribution of species, where warmer climate may trigger capelin to move northeast, and cod may follow them (their key food resource) into Russian waters (Roderfeld et al. 2008). At the same time, new species may enter the Barents Sea, leading to a new food-web in the Barents Sea ecosystem. It is easy to imagine that such changes will have severe management implications. These food-web dynamics have profound effects for both the dynamics of cod and the entire ecosystem, and as a result, the fisheries.

This simplified food-web between cod, capelin and herring show that it is not straightforward task to predict the outcome of climate change (Hjermann et al. 2007a; Hjermann et al. 2007b; Hjermann et al. 2010). Cod recruitment appears to have become more dependent on favourable climate in the year of spawning over the years (Hjermann et al. 2007a).

Figure 1. The NEA cod has its feeding ground in the Barents Sea and spawning ground along the Norwegian coast. The capelin is the most important prey species for NEA cod and its spawning ground is overlapping with the feeding ground for the cod. This figure has been originally developed by Bjørn Gjevik (Gjevik 2009) and modified by Dag. Ø. Hjermann.

Harvesting, spawning stock biomass and management

The fishing pressure shifted with the technological change in the 1930s: the fishing fleets became dominant on the feeding grounds (the Barents Sea). In some years after the 1960s, the probability of a cod caught by fishing gear could be above 70% per year on the feeding grounds (M. Heino unpublished data, Eikeset et al. 2010a). At the same time, the harvest pressure on the spawning grounds (around the Lofoten islands) decreased from 50% to 10%. However, the total fishing pressure increased and as in many other exploited stocks, the

spawning stock biomass (SSB) in NEA cod became dominated by younger and smaller fish (Marshall et al. 2006; Ottersen 2008) (Figure 2). During the last decades, the link climate–cod-recruitment has been found to become stronger (Ottersen et al. 2006). Such juvenation of the population may increase susceptibility to future changes and therefore have consequences for stocks being less robust or resilient to environmental changes (Ottersen et al. 2006).

Changes in SSB were observed by fishermen as smaller fish were caught along the Norwegian coast, because the cod that mature and migrate down to the Lofoten islands to spawn had become younger and smaller: In the beginning of the 1930s, the cod matured at the age of 9 and length at 80 cm, while today cod mature at the age of 6 and 60 cm (M. Heino, unpublished data, Eikeset et al. 2010a). Why is this happening and what has driven these changes?
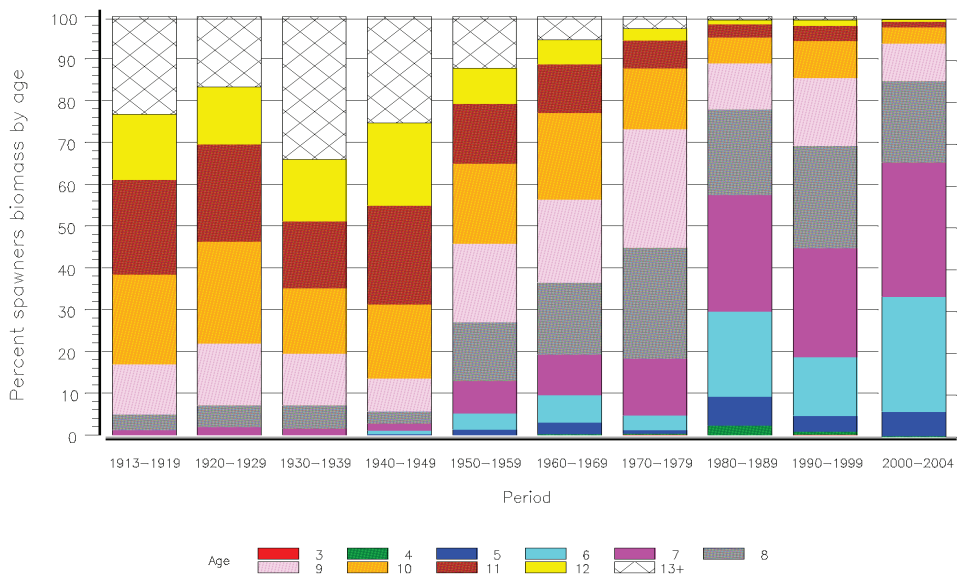
Figure 2. Decadal time-series from 1913-2004 showing the mean percentage of spawning stock biomass (SSB) by each age group. Data are on NEA cod for age 3 and older (From Ottersen 2008).
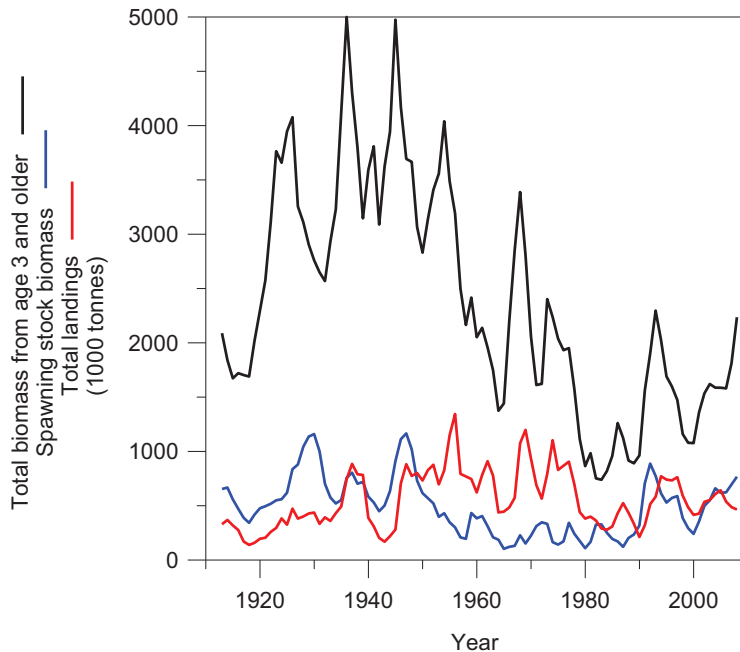
Figure 3. Total biomass from age 3 and older, spawning stock biomass (SSB) and reported landings from 1913-2008. Data from 1913-1945 are obtained from A. Hylen, from 1946-2008 data are obtained from ICES (ICES 2009a).

For 2009, ICES (International Council for Exploration of the Sea) has estimated the SSB in NEA cod to increase further from 2008 and reach 1079,000 tonnes, which has not been seen since 1947 (ICES 2009a). Although SSB has increased, the total biomass has not had this correspondingly large increase (Figure 3). In addition to possible effects of climate, this increase in SSB is mainly caused by two reasons (B. Bogstad, personal communication): first, illegal fishery has been reduced from 166,000 tonnes in 2005 to 15,000 tonnes in 2008. This decline is most likely due to the introduction of port state control in 2007 where all vessels must be cleared by the state port that their catch is legally caught. Second, a harvest control rule (HCR) that determines the total allowable catch (TAC) was agreed upon and implemented from 2004 on. This HCR derives a TAC depending on the SSB. This is to ensure that the stock is not at "risk of being harvested unsustainably" or "suffering reduced reproductive capacity". However, the advised TAC from the adopted HCR is not always followed. For example in 2009, due to the high SSB, the TAC was decided by the Joint

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Norwegian- Russian Fishery Commission to be 525,000 tonnes, while the adopted HCR advised 473,000 tonnes (ICES 2009a). Today, the stock is classified as "having full reproductive capacity" and "being harvested sustainably" (ICES 2009b; Kovalev & Bogstad 2005).

The ecological and evolutionary effects of harvesting

There are two main hypotheses for describing the observed changes in earlier and smaller size at maturation of NEA cod. The first claims that the changes are driven by ecological dynamics through phenotypic plasticity: Phenotypic plasticity is when a single genotype is expressed as multiple phenotypes (Ernande et al. 2004; Pigliucci 2005; Stearns 1989). This plasticity makes it difficult to determine if life-history traits are changing as a result of underlying genetic change, and is therefore at the heart of the debate on fisheries-induced evolution (Andersen & Brander 2009a; Andersen & Brander 2009b; Conover & Munch 2007; Darimont et al. 2009; Hilborn 2006; Jørgensen et al. 2007; Kinnison et al. 2009; Marshall & McAdam 2007). For example, when harvesting reduces the biomass levels, more resources (e.g., food) are available to the remaining fish, and this fish can therefore grow faster and reach maturation earlier. The second hypothesis claims that changes in maturation can also be driven by evolutionary changes in the life-history traits: these are caused by genetic adaptations and driven by the change in selection pressure from the fishing mortality. For example, if the risk of getting caught is high, only the individuals that mature and reproduce before they die can pass on their traits to their offspring. Therefore, early-maturing individuals are the ones favoured by evolution. To summarize these two hypotheses, one of them claims that the change in maturation is driven by ecological processes only, while the other claims that these changes are also partly driven by genetic adaptations. However, these two hypotheses are not mutually exclusive. The mechanisms driven by ecology and evolution are intertwined in a eco-evolutionary dynamics where the effects from ecological changes act on evolutionary processes, and vice versa (Pelletier et al. 2009). A small change in selection pressure may induce evolutionary changes, but may not be easily detected, which makes the relative contribution of evolutionary and ecological effects not easy to disentangle.

MAIN OBJECTIVES AND APPROACH

To investigate the effects of fishing on NEA cod, we tackle this problem from two sides: First, we focus on the population level and use data on landed catch and bottom trawl to estimate the "true" abundances and catch. At the same time, we aim to account for uncertainty about effects of components driving the population dynamic, by including both observation uncertainty and process error. We then try to derive knowledge about natural mortality and density-dependence. Hence in Paper 1, *Destabilized population growth rate in Northeast Arctic cod*, we investigate how population growth rate has developed over time in NEA cod and how this may be affected by climate, fishing, and density-dependent mortality. Then, we test through stochastic simulations if variability in fishing pressure may lead to larger fluctuations in stock size.

Our second approach to study the effects of harvesting starts at the individual level to derive knowledge about the population level. Changes at the individual level progressively affect the population level. We do this by developing an individual-based model, which is ecologically and genetically detailed, and based on data for the NEA cod. The model has been developed to resemble the life-cycle of the cod to study if there are evolutionary changes in life-history traits (i.e., maturation) caused by the observed fishing pressure from 1932 until 2005. The genetic component in this model allows the individuals to respond to selection pressure brought about by fishing pressure. At the population level, mechanisms such as density-dependent growth and newborn survival, temporal variability in recruitment and mortality act on the population, being observed by younger and lower biomass level over the course of fishing. We ask whether fisheries-induced evolution have occurred in NEA cod from 1932-2005. Can we find evidence for the hypothesis claiming that the observed phenotypic changes in maturation are also driven by evolutionary response to the selection pressure? If it does, how large and fast are these evolutionary changes? This is the focus of Paper 2, *Is evolution needed to explain historical maturation trends in Northeast Atlantic cod?*

Can fisheries-induced evolution affect the economic yield, and how does it change optimal management strategies? This is the focus of Paper 3, *The economic repercussions of fisheries-induced evolution*. Paper 4, *A bio-economic analysis of alternative harvest control rules for Northeast Arctic cod in the light of the precautionary principle - a counterfactual scenario*, takes a step back in time and investigates if there are better ways of managing the stock than what has been historically done. Looking forward from 1932 until 2005, we

compare economic and biological consequences of three alternative HCRs: (1) the economic income or yield is maximized, (2) the precautionary HCR advised by ICES, and (3) the HCR agreed upon and implemented since 2004 for NEA cod.

Finally, Paper 5, *Unintended consequences sneak in the back door: making wise use of regulations in fisheries management*, is not a modelling paper, but a qualitative discussion. By taking a broad overview we here examine some of the complexities brought about from the biological and social system, which might be difficult to see, and also, not easy to learn about.

Population level

Hsieh et al. (2006) and Anderson et al. (2008) found that exploited fish stocks show larger fluctuations than unexploited. Both studies used time-series on ichthyoplankton (e.g., fish larvae) data as a proxy for fish biomass. Even though this proxy has shown to be quite good (Hsieh et al. 2006), there is as in any study, a risk that uncertainty in the data and lack of information may have masked the observed mechanisms behind the phenomenon one considers. To make reliable projections about the state of the stock (i.e., true abundance, natural mortality) observation uncertainty and process error should be accounted for (Aanes et al. 2007). The effect of environmental noise on population size must be disentangled from stochasticity caused by uncertainty in parameter estimates (e.g., natural mortality) and errors in estimates on population size (Freckleton et al. 2006; Aanes et al. 2007). In marine science and stock assessment, state-space modelling has become a popular modelling framework that can be developed to include parameters that describe expected dynamics, as well as stochastic influences (Bogaards et al. 2009; McAllister & Carruthers 2007; Millar & Methot 2002; Millar & Meyer 2000a; Millar & Meyer 2000b; Millar & Stewart 2005; Swain et al. 2009; Aanes et al. 2007).

Today, catch data are used to back-calculate abundance by adding fishing and natural mortality, and then calculate what the abundance the year before was; this is called Virtual Population Analysis (VPA, including methods such as XSA, ICA and ADAPT) (ICES 2009a). Survey data can also be included, adding more realism (Shepherd 1999). The challenge is that even if survey abundance indices may be biologically very realistic, they are indices (not absolute population estimates), and only snapshots of the population size. Therefore, catch data and survey data are at a different scale and are most often not easy to unite. For this issue, state-space models have proven to be very useful.

In paper 1, *Destabilized population growth rate in Northeast Arctic cod* (Eikeset et al. 2010b) we developed a state-space age-structured model for NEA cod using data on abundance from survey and catch statistics for the period 1981-2007. VPA analysis provide estimates on abundances from age 3 (ICES 2009a). Our model produces estimates on the "true" age-specific abundance and catches, including abundances for the youngest age-classes 1 and 2 –year olds. In this process, the model also predicts variability in natural mortality, observation and measurement uncertainty and process error in the population dynamics. We find that increased variability in fishing mortality can lead to larger variability in SSB. This is supporting a previous study by Jonzen et al. (2001), but they used data from VPA analyses. Andersen et al. (2008) did not find support for this hypothesis, but found that it is the increase in mean fishing mortality that lead to increased fluctuations and non-linear population dynamics. We demonstrate that variation in fishing, climate and density-dependent mortality strongly affects the variability in population growth rate. First, density-dependent mortality is important in the youngest age-classes and as expected from ecological theory (Begon et al. 1996), density-dependent mortality may act compensating on the population growth rate. Second, it is not the extent of fishing mortality that leads to destabilised fish stocks, but large year-to-year variation. This is of prime concern because if neglected in population models such mechanisms can generate biased predictions. Hence, high fishing mortality does not create fluctuations per se, it is merely causing a constant decline (from the reference level, i.e. 1981 level) if mean fishing mortality exceeds 0.7 year^{-1} in NEA cod. Third, variations in recruitment, which may come about through climate effects, increase the variability in population growth rate.

From individual level to population level

"Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1964). In paper 2 we ask: *Is evolution needed to explain historical maturation trends in Northeast Atlantic cod?* (Eikeset et al. 2010a). Here we investigate if fisheries-induced evolution has occurred in NEA cod from 1932-2005. Following this mechanism, a change in fishing pressure leads to a change in selection pressure: before the 1940s when fishing pressure was low in the feeding ground and high in the spawning ground, selection pressure was favouring large size at maturation, so the large and old fish migrated to spawn the spawning ground along the Norwegian coast (Figure 1). Larger sized fish have higher fecundity through larger gonads (Kjesbu et al. 1998; Marshall et al. 2006). Hence, it pays off to delay sexual

maturation, so when reproducing, the number of offspring is likely to be high. This is natural or harvest-induced selection towards larger size at maturation. However, after the 1940s when fishing pressure in the feeding grounds increased, immature fish (e.g. smaller size) were also caught. Under these new conditions, it became advantageous to grow faster and mature earlier, in order to increase the probability to mature and reproduce before death. In terms of reproductive output, it was now risky to wait with maturation. Therefore, in this case, harvest-induced selection for small sizes at maturation occurs.

"Nothing in evolution or ecology makes sense except in the light of the other" (Pelletier et al. 2009). Our life-history model describes every individual's life-cycle through four processes: growth, maturation, reproduction and mortality. It is parameterised specifically for NEA cod and is novel in the sense that it is a complex life-history model and uses many sources of data describing a real stock over a 74 years period. For a specific wild and exploited stock it can predict to what extent fisheries-induced evolution occurs when phenotypically plastic maturation and growth are accounted for: We impose the historic fishing pressure, mimicking what has happened to the stock, and then compare our simulation predictions with data on age and length at maturation for the period, 1932-2005. By manipulating the level of genetic variation assumed in the model, we determine how much evolution is required to match historical trends in the age and length at maturation. We find that fishing has ecological and evolutionary effects, but the extent of how much evolution is needed, depends on complex dynamics between ecology and evolution: a model with evolution is better in replicating historical trends than a model without evolution. Furthermore, fisheries-induced evolution, in particular of increased growth, may prevent stock collapse, but the match with historical data depends on the density-dependent growth model used. We also find that although an evolutionary model outperforms a non-evolutionary model, the amount of evolution of traits is predicted to be smaller than suggested in previous studies.

Costs and benefits of fisheries-induced evolution

One worry for evolutionary changes has been the lack of recovery and decrease in yield. Given that fisheries-induced evolution has already occurred in the past, what would be the best way to avoid additional undesired effects in the future? If evolutionary effects are present, but ignored by managers, how costly will it be to overlook fisheries-induced evolution? We try to answer these questions in paper 3, *The economic repercussions of*

fisheries-induced evolution (Eikeset et al. 2010e), by combining ecology, evolution, and economics to evaluate optimal harvest scenarios when including accurate economic data based on the Norwegian fleet. Our results show that fisheries-induced evolution decreases economic yield if fishing mortality is too high. In contrast, the economic income is higher if fishing mortality is lower: an optimal HCR improves the historic fishing pressure from 1946-2005, it boosts economic profits and reduces changes in age and length at maturation. In this case, fisheries-induced evolution decrease age and length at maturation, but increases the SSB and therefore the economic yield. We find that low fishing mortality is the key to higher SSB and economic yield, with or without addressing evolutionary changes. Unfortunately fish stocks are typically far from being managed optimally and high fishing mortality is very common. We find that the interplay between ecology and evolution changes life-history traits and stock properties, and therefore economic income.

The objectives determines the optimum catch

In paper 4, *A bio-economic analysis of alternative harvest control rules for Northeast Arctic cod in the light of the precautionary principle - a counterfactual scenario* (Eikeset et al. 2010c), we compare alternative harvest control rules (HCRs) with the observed fishing mortality from 1932-2005. The alternative HCRs are derived from 1) optimal HCRs that have maximized yield or economic income 2) the precautionary HCR advised by ICES, 3) the implemented HCR for the cod fishery. We find that these produce different harvest patterns in terms of fishing mortality, biomass, catch and profit. For example, if profits are maximized, the catch is lower. This is because of the price effect, where lower catch gives a higher price. As a result, the consumers pay higher prices and buy less fish. The decision what to maximize, and what the objectives should be, is a political choice. We discuss how the economic success for the fishery requires biological sustainability, and how results obtained from an optimization routine perform in the light of the precautionary principle.

Integrated management

In paper 5, *Unintended consequences sneak in the back door: making wise use of regulations in fisheries management* (Eikeset et al. 2010d), we discuss management tools and highlight that their adequacy depends on the specific system, the costs of implementation and the difficulty to obtain all relevant information. Ostrom (2009) classified a social-ecological

system by its subsystems: (i) resource system (e.g. the cod fishery), (ii) resource units (e.g. NEA cod), (iii) users (e.g. fishermen), and (iv) the governance system (e.g. the specific laws and social norms in place). The first step in management is to identify these components with their characteristics and then determine what is relevant for making policy recommendations. However, one of the most difficult tasks is to identify and quantify these specific systems and their attributes. For example, for a given stock, a HCR is a rule for setting the annual quota and depends on the biomass level of the stock. However, biomass is never exactly known, but always uncertain. Therefore, dealing with uncertainty in the biological system and incorporating this into precautionary management is a challenge. Another question is who should be involved in the management process, and should the participants be made more responsible? Often, there is a trade-off between making decisions now and wait with acting until more knowledge is reached. Some stocks are to such an extent threatened by extinction, and so waiting for more knowledge may be a very dangerous strategy. The precautionary principle is clear in theory, but when and how should it be applied?

SIMULATIONS

Fallibility is the hallmark of science (Kitcher 1998). Every observation is guided by theory, with hypotheses being intellectually constructed conjectures that can be conclusively falsified in the light of suitable evidence (Chalmers 1999; Kitcher 1998). However, whatever the evidence, theories can never be established as true. To test 1) do fisheries-induced evolution occurs in a real stock and 2) are the economic effects of such evolutionary changes important, and 3) how far away we are from optimal management, we used numerical analyses to make predictions. We consider simulations as metaphysical, where our numerical model creates a parallel world (Frigg & Reiss 2009) in which "experimentation" can be performed, theories can be falsified and real life experimentation fails. Another advantage with simulations is that robustness and consistency of results can be thoroughly checked by replication (Galison 1996) and sensitivity analysis. Scientists may only "arrive at partial and incomplete truths. Numerical analysis of data carry the deduction through many steps and it is as such crucial to 'keep the argument straight'" (Ziman 1968).

Challenges arise when comparing our results to the real world. Can we be sure that these simulations represent reality? An increasingly widespread position is that numerical analysis represents the world because the world itself is probabilistic. In our case, one

message to managers could be that fisheries-induced evolution is a crucial force in driving stock dynamics and avoiding stock extinction. Equally, another message could be that fisheries-induced evolution is not crucial for stock survival, but adding it into the model explains the data better. The need to decrease fishing pressure is not only justified by evolutionary changes. Also other influences shape the population, such as environmental change and density-dependence. Nevertheless, the extent to which each of these components shapes the stock must be discussed.

Science is maybe strongest when it fails, then we can say *this is not the way it is*. As long as the model stands the test against data, uncertainty is attached to it. If the model, with its uncertainty, can guide management to reach sustainability, then the argument for taking the model into account is stronger than rejecting it. Such ethical arguments should be considered when addressing the model's value. This is because models are explanatory, not true.

CONCLUSION

The NEA cod population is reported to be in good shape (ICES 2009a) but it is important to look beneath the surface to ensure sound management and to avoid unpleasant surprises in the future. This can be summarised in one simple quote by Rosemary Grant, Kyoto Prize winner 2009 at the Kristine Bonnevie lecture 2009: "Neither species nor environments are static entities, but dynamic, and constantly changing. To conserve species and their environments, we must keep them both capable of further change." The NEA cod stock is no exception in this regard.

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