Running head: Capelin variability amplifies cod instability

Managing Arctic predator harvest instability amplified by variable prey productivity and ocean temperature

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Abstract

Living marine resources are often managed for single target species under precautionary harvest policies to achieve socioeconomic and conservation objectives through a tradeoff between short-term yield stability and long-term sustainable harvest. However, not accounting for imperfect knowledge of how dynamic ecosystem processes modulate variability in fished populations (ecological uncertainty) may underestimate risks of missing management targets. We present an illustrative case study to test how constraining short-term fluctuation in catch quotas perturbs stock and yield stability of an apex predator, Northeast Arctic (NEA) cod (*Gadus morhua*), when its primary food resource, capelin (*Mallotus villosus*), and climate vary over time. We use a stochastic multispecies model (STOCOBAR–*Stock of Cod in the Barents Sea*) to simulate the cod stock dynamics through life history processes under variable ocean temperatures. Capelin productivity influences cod biomass directly through consumption and indirectly through cannibalism by adult cod. We evaluate harvest strategy scenarios of varying levels (5% to 50%) of yield stability constraints under the current precautionary harvest control rule (target exploitation rate, F_{pa}, of 0.40 and threshold spawning stock biomass, B_{pa}, of 460 thousand tonnes). Analyses show that performance of constraining catch fluctuation is highly sensitive to how cod and capelin interact. When the constraints are tightened to 25 % or less, the stock abundance and catch are projected to rise while the year-to-year variation is amplified through variable cod cannibalism–capelin productivity. Our work reveals that muffling variance in catch forces cod to respond to capelin fluctuation faster, becoming increasingly unsynchronized with harvest intensity and, thus, increasing recruitment variability and facilitating stock depletion (higher probabilities of exceeding F_{pa} and falling below B_{pa}–21% and 15%, respectively). Our study demonstrates unintended consequences of stability control of fish catches, a commonly adapted harvest strategy in industrial capture fisheries. This policy can

inadvertently destabilize stocks, amplify catch fluctuation, and ultimately increase overharvest risk when not accounting for compounded effects of ecologically connected processes in assessments, underscoring the need for an ecosystem approach to designing management strategies to safely harvest top predators in increasingly more dynamic oceans.

KEYWORDS: management strategy evaluation; food web; ecosystem-based management; forage fish; stock assessment; recruitment; climate variability; cod

INTRODUCTION

Fluctuation in living natural resources poses myriad socioeconomic and conservation challenges in sustainably managing harvest (Fryxell *et al.* 2010; Carpenter *et al.* 2015). Stable marine resources provide not only predictable quotas to harvesters but also food and employment security in many fishing nations (Garcia & Rosenberg 2010). In industrial capture fisheries, harvest strategies are designed to maintain stock abundance above a threshold that prevents overharvest and sustains its fishery; however, some harvest rules (for example, constant escapement rules) can amplify year-to-year catch fluctuation (Deroba & Bence 2008). To achieve short-term stability in catch, additional control rules are often set to constrain the variation (Deroba & Bence 2008). Such control rules are currently developed and implemented for single target species, assuming stable biotic and abiotic conditions (Hall & Mainprize 2004). However, these assumptions are often violated in oceans; fluctuation in ecosystem productivity may amplify variability in fished populations (May 2001; Rouyer *et al.* 2012). Harvest strategies that fail to account for dynamic ecosystem processes may, thus, lead to exploitation rate that is unsynchronized with natural stock dynamics, increasing the risk of overfishing and stock depletion (Mace 2001; Hall & Mainprize 2004), and socioeconomic damage (Caddy & Seijo 2005; Nielsen *et al.* 2018).

Variability in fish stocks can arise from stochasticity in demographic traits under dynamic environments (Ware & Thomson 2005; Pepin 2015). These dynamics often propagate

through trophic interactions to modulate productivity of fished populations (Ottersen *et al.* 2001; Ware & Thomson 2005). Environmentally driven plankton production, for example, regulates forage fish production that support fished apex predators (Ware & Thomson 2005; Frederiksen *et al.* 2006). Large year-to-year fluctuation can emerge particularly in early life stages of marine populations (Leggett & Deblois 1994; Ottersen & Loeng 2000); seasonal to decadal variation in ocean conditions propagates through predator–prey interactions, amplifying or dampening variance in year-class strength of exploited predators (Edwards & Richardson 2004). Uncertainty in trophic dynamics can, thus, pose challenges in designing control rules to maintain yield stability for exploited populations (Essington, Sanchirico & Baskett 2018).

Trophic interactions between cod (*Gadus morhua*) and capelin (*Mallotus villosus*) in the North Atlantic present such dynamics that modulate year-to-year fluctuation in cod fishery yield (Link *et al.* 2009). Cod productivity often fluctuates from year to year with variability in ecosystem (bottom-up) processes including interactions with other fishes during early life stages (Lilly *et al.* 2008; Minto & Worm 2012). In particular, cod cannibalism is often amplified by food shortage (Yaragina, Bogstad & Kovalev 2009); capelin–a short-lived (≤ 5 years), semelparous, widely distributed pelagic planktivore–comprises a large part of adult cod diet (Dolgov 2009; Holt *et al.* 2019) and may regulate cod cannibalism on the young (age ≤ 3) and, in turn, recruitment dynamics. Moreover, owing to migratory behaviors driven by ocean conditions and plankton distribution, time-varying capelin aggregation may reflect changes in ecosystem processes including systemwide shifts in ice phenology, thermal regimes, and plankton productivity (Carscadden, Frank & Leggett 2001; Rose 2005). Spatial and temporal overlap between cod and capelin in cod spawning and nursery grounds may, thus, regulate cod recruitment, stock structure, and yield variability (Ciannelli & Bailey 2005; Johannesen *et al.* 2012).

The Northeast Arctic (NEA) cod stock distributed over the Barents Sea and its surrounding areas (Fig. 1a) is the world's largest, supporting two major fishing nations, Norway and Russia (Kjesbu *et al.* 2014). The fishery dates back to the period when the northern coasts of these nations were likely populated after the end of the last ice age. An international industrial trawl fishery in the Barents Sea developed in the early 1900s and total catches by all gears peaked at more than 1.2 million tonnes in catch in some years in the period 1955-1975 (ICES 2019). Following the establishment of 200-mile economic zones in the late 1970s, the fishery by Norway and Russia dominated (ICES 2019) and subsequently depleted the stock prior to the establishment of a harvest control rule (HCR) by the Norwegian-Russian Fishery Commission in the early 2000s (ICES 2019). This HCR, which was in force until 2016, the target exploitation rate (that sustainably maximize yield) at 40% of harvestable stock biomass. Further, to constrain yield fluctuation, 1) the catch quotas are set for the three coming years (as averages); and 2) year-to-year yield fluctuation is limited to less than 10%. These harvest strategies, along with favorable habitat conditions, ultimately allowed the stock to balloon with the quota reaching one million tonnes in 2014, the highest in more than three decades (Kjesbu *et al.* 2014). However, it remains uncertain how the harvest strategy of constraining year-to-year yield fluctuation would perform and contribute to stock behavior if variable ocean conditions were accounted for.

Here we illustrate how the harvest strategy of constraining year-to-year yield fluctuation regulates short-term stability in catch and long-term stock persistence when accounting for ecological (structural) uncertainty, time-varying ecosystem productivity, with NEA cod as a case study. Using a stochastic, multispecies model previously developed for the Barents Sea cod–capelin complex (Filin 2009; Howell *et al.* 2013), we analyze harvest strategy scenarios designed to constrain year-to-year fluctuation in NEA cod yield (ICES 2016) with time-varying capelin biomass (Fig. 1b)–a proxy for the Barents Sea ecosystem carrying capacity

(Gjøsæter 1998) under variable ocean temperature (environmental stochasticity, Fig 1c). We further test how the cod harvest strategy performs when incorporating an ecological mechanism that regulates cod year-class strength–an interplay of cod cannibalism and capelin variability (Hjermann *et al.* 2007), and evaluate implications of adapting the ecosystem-based approach to conservation and sustainable use of marine fish stocks under climate variability.

MATERIALS AND METHODS

Barents Sea cod–capelin system

The Barents Sea cod–capelin complex is among the few co-managed stocks in the North Atlantic (Gjøsæter, Tjelmeland & Bogstad 2012). Historically, capelin has been the major forage species supporting exploited apex predators in the Barents Sea food web (Gjøsæter 1998); its stock biomass has been measured by acoustic methods to reach up to seven million tonnes in the 1970s and 1990s (Gjøsæter 1998). Capelin is a small, pelagic, schooling fish, rarely reaching lengths above 20 cm and ages above five years. It feeds in the northern Barents Sea on meso- and macro- zooplankton but migrates to the northern coasts of Norway and Russia to spawn in spring. It is semelparous and thus magnifies its role of bringing energy from the northern parts of the Barents Sea to the southern coastal areas. Although capelin supplies a food source for many piscivores in the Barents Sea, cod are by far their primary predator, consuming up to more than three million tonnes per year (Dolgov 2002). Capelin fluctuation, thus, likely drives the intensity of cod cannibalism and year-class strength, reflecting depensatory effects of depleted food resources (Hjermann *et al.* 2007). For example, amplified year-to-year fluctuation in capelin biomass in the 1980s and 1990s was largely responsible for the cod stock development; cod cannibalism peaked following the capelin collapses (Hjermann *et al.* 2007). The collapses, in particular the first one, propagated through the rest of the Barents Sea food web to a variable degree, depending on availability of other food (Hjermann *et al.* 2007; Gjøsæter, Bogstad & Tjelmeland 2009).

Barents Sea cod-capelin model

To simulate the Barents Sea cod-capelin dynamics, we used a stochastic, multispecies model that accounts for ecosystem processes (a model of intermediate complexity for ecosystem, Plagányi *et al.* 2014)–STOCOBAR (***Sto**ck of **Co**d in the **Bar**ents Sea*). STOCOBAR has been developed previously at Russian Federal Research Institute of Fisheries and Oceanography (Filin 2009); the version used in this study has been described fully in Howell *et al.* (2013) (Fig. 1d). The model was fitted to time series (1981–2010) data of cod abundance (annual bottom trawl and acoustic survey) indices (CPUE), catch, capelin biomass, maturity-at-age, and weight-at-age, which were taken from annual stock assessments by the International Council for the Exploration of the Sea (ICES) Arctic Fisheries Working Group; the methods used are extensively documented in ICES (2010). For brevity, we outline the model structure here; STOCOBAR simulates age-structured population dynamics of the cod stock in a single area (Barents Sea and adjacent areas) with a single fleet through yearly growth, feeding, maturation, recruitment, natural mortality (including cannibalism), and fishing mortality (Howell *et al.* 2013). Growth and feeding are temperature-dependent to capture variable metabolic rate (Fig. 1d, Howell & Filin 2014). The model projects cod stock development and evaluates harvest strategies and recovery plans under plausible ecosystem scenarios including trophic dynamics between cod as a predator and one or more prey under climate variability (Howell *et al.* 2013).

We used capelin biomass as a proxy for the carrying capacity for cod, representing “good” and “poor” years of habitat conditions that regulate cod growth and cannibalism. The model uses capelin as a primary food source for cod with all other food items being aggregated as “other food’. Capelin were statistically modeled (no feedback for cod predation on capelin, Fig. 1d) to simulate observed patterns of declining biomass 1) when cod spawning stock biomass (SSB) exceeding 400 thousand tonnes or 2) when capelin biomass falling below

three million tonnes in the previous year. Further, we imposed a cap on capelin biomass at six million tonnes when cod SSB exceeds 800 thousand tonnes. The modeled capelin biomass varies among years and simulations (on average, from 684 to 2789 thousand tonnes, Fig. 1c).

Cod recruitment (at age 3) depends on age-1 cod abundance and cod cannibalism. Age-1 cod abundance is simulated using the Ricker stock-recruitment function, and pre-recruit mortality by cannibalism is a function of capelin biomass and cod stock structure (size and age composition) (Fig. 1d, Howell *et al.* 2013). Although temperature may affect cannibalism indirectly through consumption, this effect is negligible within the historical temperature range used in this study. Further, we did not include indirect temperature effects on cannibalism through spatial distribution (Howell & Filin 2014). Based on the model fitting, we capped mortality by cannibalism at 90%, 60%, and 40% of total mortality at age- 1, 2, and 3 (respectively). Uncertainty in recruitment was then incorporated using residuals in the simulated data for the historical period of 1980–2007, assuming the normal distribution.

Ocean temperatures regulate the model cod stock dynamics through recruitment, growth, and consumption (Fig. 1d). The model uses a thermal regime that replicates historical patterns of annual temperature changes in the Kola Section in the Barents Sea (Fig. 1b). To create a temperature scenario, we first split the observed temperature data (1950-2017) into three groups; cold (annual mean temperatures < 3.6°C), moderate (3.6°C ≤ annual mean temperatures ≤ 4.2°C), and warm (annual mean temperatures > 4.2°C) years. Then, temperature data were randomly selected from these three groups sequentially. The modeled periods (cold, moderate and warm years) last from one to five years; the length of each period was set randomly (Fig. 1b).

Harvest control rules (HCRs) for NEA cod

We evaluated modeled NEA cod stock behaviors based on the precautionary approach to HCR performance of the 2016 TAC calculation (ICES 2016). Under this HCR, mean

instantaneous fishing mortality rate of age 5–10 fish (F_{bar}) is set to 0.40 (F_{pa}) when SSB equals to or exceeds 460 thousand tonnes (B_{pa}). When SSB falls below B_{pa}, F_{bar} is set to F_{pa} scaled to the proportion of SSB relative to B_{pa} as:

$$F_{bar} = F_{pa} \frac{SSB}{B_{pa}}$$

Annual fishing mortality rate at age is computed as:

$$F_{ji} = \frac{F_{bar(i)}}{F'_{bar}} F'_j ,$$

where F_{ji} is fishing mortality rate at age of j in year i; $F_{bar(i)}$ is mean fishing mortality rate in year i, computed in the model according to the set HCR; F'_{bar} is mean fishing mortality rate in the initial year; and F'_j is fishing mortality rate at age j in the initial year.

The harvest rule to constrain yield fluctuation provides stability and predictability for harvesters by minimizing year-to-year variability in catch (and thus revenue). Under the precautionary principle, the stability constraint is applied only when SSB equals to or exceeds B_{pa}. If this results in TAC year-to-year variation exceeding the set constraint (±%), the model algorithm searches for F_{bar} until it finds the value that does not exceed the boundary set by the constraint. The constraint was not applied in the first year after the recovery period (when SSB < B_{pa}); F_{bar} is set to F_{pa} regardless of TAC in the previous year. The 2016 management strategy evaluation of this HCR with year-to-year variance in TAC constrained to ±10% has demonstrated that implementing the stability constraint (with density dependence in cannibalism and growth) under constant productivity reduces interannual variability in cod catch by more than 50%; however, mean SSB declines by nearly 15%, and the risk of overharvest rises 2x (ICES 2016). To evaluate how constraining short-term variation in TAC influences the cod stock behavior and catch stability under variable capelin productivity and climate, we analyzed nine management scenarios to constrain year-to-year variation in cod

catch–no constraint (±0%), ±5%, ±15%, ±20%, ±25%, ±30%, ±40%, and ±50% with varying capelin biomass and, in turn, cod cannibalism intensity. We used the following performance metrics to evaluate the harvest strategies; SSB, total (age 3+) stock biomass (TSB), TAC, interannual catch variability, and risks–probabilities exceeding precautionary reference points (B_{pa} and F_{pa}) and limit reference points (B_{lim} = 220 thousand tones and F_{lim} = 0.74).

To further evaluate how process (ecological) uncertainty involving capelin variability–an interplay of capelin variability and cod cannibalism–contributes to cod catch variance under stability constraints, we tested model performance of four model configurations that represent ecological assumptions on cod cannibalism–capelin variability under a 10% constraint and variable ocean temperature; 1) varying capelin biomass with cannibalism, 2) varying capelin biomass without cannibalism, 3) constant capelin biomass (1000 tonnes) with cannibalism, and 4) constant capelin without cannibalism.

We ran 100-year simulations to evaluate each management scenario (25 x 9 simulations). We analyzed each scenario based on 25 realizations because preliminary simulations showed that mean catches vary less than ±1% with more than 25. We disregarded the first 20 years of model output as a 'burn-in' to minimize effects of the initial conditions and evaluated the outputs from year 21 to 100. Because this study primarily focuses on implications of applying limits to year-to-year fluctuations in cod catch, we did not incorporate other sources of uncertainty such as assessment error and implementation error (annual catches are assumed equal to TAC) in this study; we set fishing selectivity (fishing pattern) as time-invariant in the first year. Further, for clarity, we simplified the cod HCR in simulations by removing the following constraints; the "three-year forecast", F applied to current SSB to compute TAC, the floor of F = 0.3, and setting the target F (=1.5x F_{pa}) when SSB exceeds 3x B_{pa} (ICES 2019).

RESULTS

Cod stock performance and yield stability

Under the base scenario, projected cod biomass reached dynamic equilibrium by year 20 (Fig. S1), with mean stock size (TSB) of ~2.3 million tonnes, mean spawning stock biomass (SSB) of ~1.1 million tonnes, mean catch of 680 thousand tonnes, and 694 million recruits (Table 1), which are all in line with the historical stock status of NEA cod (ICES 2017). With higher than 30% constraints, the stock showed negligible changes (Fig. 2 and S1). By contrast, with 30% or lower constraints, SSB and catch became increasingly variable with greater amplitudes (Fig. 2 and S1). The stability rule was implemented increasingly more often as the constraints became tighter (33%, 48%, and 72% of the projection years under 30%, 20%, and 10% constraints scenarios, respectively). Further, mean your-to-year (and overall among-year) variation in stock size, SSB, and recruits rose (by, on average, 44%, 69%, and 116%, respectively, Fig. 3). The management strategy evaluation of the cod HCR, which based on an assumption of constant capelin production, has showed that mean year-to-year variation in catch declines from 26.9% to 12.4% (with a decline in mean catch from 777 to 744 thousand tonnes) with the 10% constraint (ICES 2016). By contrast, with variable capelin productivity, mean year-to-year variation in catch and fishing mortality rose, ranging from –39% to 166% and –24% to 96% (respectively); catch varied from 142 to 1234 thousand tonnes, whereas fishing mortality varied from 0.18 to 1.1 (Fig. 3).

Stock size–fishing mortality asynchrony

Temporal patterns of cod stock abundance and fishing mortality became increasingly asynchronized, accompanied by shorter periods and larger amplitudes with 30% or lower constraints (Fig. 4). With the 10% constraint, fishing mortality became increasingly more variable as constraining catch led to overharvest more often, peaking at the lowest stock abundance (250 thousand tonnes) in year ~75, and then stabilized with fishing mortality at F_{pa} (Fig. 4).

Cod cannibalism–capelin productivity interaction

Incorporating time-varying capelin biomass amplified year-to-year variation in cod stock (through changes in consumption and cannibalism intensity) and catch. When capelin biomass was time-invariant with no cod cannibalism, year-to-year variation in cod catch remained less than 2% even under the 10% constraint (Fig. 5 and S2). Likewise, with varying capelin biomass and no cod cannibalism, catch variation rose by only ~4% (Fig. 5 and S2). By contrast, when cod cannibalism was introduced, catch variation varied from –56% to 70%. When varying capelin biomass and cod cannibalism were both introduced, catch variation rose further, ranging from –90% to 312% (Fig. 5 and S2).

Stability–yield tradeoffs under variable capelin productivity and ocean temperature

Although cod stock abundance and catch both increased as the constraints became tightened from 50% to 5% (by 40% in TSB, 51% in SSB, and 17% in catch, Fig. 6a, Table 1), the harvest strategies became increasingly less precautionary (Fig. 6a). With 30% or higher constraints, mean fishing mortality exceeded F_{pa} and F_{lim} with less than 3% and 1% probability, respectively, and SSB fell below B_{pa} and B_{lim} with less than 2% probability (Fig. 6b). By contrast, with 30% or lower constraints, greater amplitudes in fishing mortality while cod biomass was declining increased the risk of overharvest and stock depletion; the probabilities of SSB falling below B_{pa} and B_{lim} (3.1–20% and 0.3–6%, respectively) and fishing mortality exceeding F_{pa} and F_{lim} increased (10–24% and 0.3–8.7%, respectively) because of asynchronized stock–fishing mortality dynamics (Fig. 4 and 6b). These risk levels with variable capelin productivity were up to 600x larger than with constant capelin productivity estimated previously (ICES 2016).

DISCUSSION

We demonstrate that constraining year-to-year variation in fishery yield can inadvertently destabilize stock and catch dynamics when not accounting for ecological uncertainty such as

dynamic predator–prey interactions and environmental stochasticity. This undesirable consequence of stability constraints as a harvest policy arises because the constraints allow fishing intensity and stock abundance to become unsynchronized owing to pronounced boom-and-bust cycles of exploited populations (Frank *et al*. 2016). In the case of Northeast Arctic (NEA) cod, unlike the findings from the latest management strategy evaluation (ICES 2016), our analyses show that variability in capelin production and ocean temperature amplifies year-to-year variation in cod recruitment through cannibalism and, in turn, stock abundance and catch under the harvest strategy investigated. Incorrect ecological assumptions of capelin variability and cod cannibalism can substantially underestimate stock variability and yield stability. Constraints of less than 30% year-to-year fluctuations theoretically produce greater cod catches in some years because of larger peaks in stock abundance and recruitment under variable capelin productivity. However, these constraints also systematically shorten cod stock periodicity when capelin productivity and ocean temperature vary over time, increasing the risk of overharvest and depletion (by up to more than 20%) under the current management plan.

Myriad ecosystem processes regulating fish survival interactively influence how harvest strategies perform in practice (Okamoto, Schmitt & Holbrook 2016). Constraining short-term yield variation disrupts fished population cycles and, in turn, inadvertently promotes larger fluctuation in catches when ecosystem productivity varies. Catch stability constraints asynchronized with ecosystem carrying capacity of the stock, for example, can amplify its variability instead (Link 2017). In relatively species-poor, high-latitude systems such as the Barents Sea, changes in productivity likely propagate further through the food web (less buffering) and may amplify year-to-year fluctuation in life history events of fished populations (Bellingeri & Vincenzi 2013). Our study uses capelin biomass as a proxy for the carrying capacity for NEA cod and its fishery. By explicitly accounting for one of the key

ecological processes that regulate cod productivity–an interplay of cannibalism and food supply, analyses reveal that dampening amplitudes in cod catch amplifies its response to capelin's shorter population cycle through cod cannibalism, forcing the population to become increasingly asynchronized with fishing intensity. Because many industrial capture fisheries selectively remove larger and older fish, greater fishing mortality in depleted stocks can further truncate age structure (Okamoto, Schmitt & Holbrook 2016; Gamelon, Sandercock & Sæther 2019). As a result, exploited populations become increasingly more recruitment-dependent, eroding their resilience to environmental stochasticity (Minto, Myers & Blanchard 2008; Gamelon, Sandercock & Sæther 2019).

Year-class fluctuation of many fished populations is governed by temporal variability (including multidecadal regime shifts) in various oceanic processes (Cushing 1990), which are often mediated through food-web interactions (Lilly *et al.* 2008). Stocks may, in turn, be overfished in poor years and underfished (yield loss) in good years if managed without accounting for ecosystem variability (Link 2017). Our analyses show that when NEA cod recruitment dynamics are strongly regulated by capelin productivity, cod stock abundance becomes increasingly variable and asynchronized with fishing intensity under tighter yield stability constraints, thereby amplifying cod catch instability. Over the past half century, the Barents Sea has shown large fluctuations in productivity (Dalpadado *et al.* 2012), during which the capelin stock has collapsed three times (Gjøsæter, Bogstad & Tjelmeland 2009). The capelin stock collapses subsequently intensified cod cannibalism, weakening cod recruitment strength (Yaragina, Bogstad & Kovalev 2009; Yaragina, Kovalev & Chetyrkin 2018), and ultimately depleting the cod stock in the late 1980s. Because Barents Sea capelin also supports other apex predators as a primary food source (as well as its fishery), its declines may have triggered a series of trophically mediated processes that exacerbated the cod stock depletion, including increased consumption of the young by marine mammals such

as harp seals (Bogstad *et al.* 2015). Cod overharvest can also release mesopredators from predation (Hjermann *et al.* 2007), promoting resource competition with and predation on young cod–weakening the 'cultivation' effect (Walters & Kitchell 2001). These complex, ecological dynamics that regulate year-class strength of fished populations can have both stabilizing and destabilizing effects under variable fishing pressure and ecosystem productivity (Anderson *et al.* 2008), confounding the performance of harvest strategies.

Imposed stability constraints may inadvertently amplify variability of exploited populations by modifying natural cycles owing to various sources of uncertainty often overlooked in assessments (Botsford, Castilla & Peterson 1997). Nearly 70% (of 200+) assessed fish stocks worldwide has shown irregular temporal shifts in productivity regime (Vert-pre *et al.* 2013); imposing constraints without accounting for ecological uncertainty such as dynamic ecosystem processes would, thus, likely increase the risk of overharvest and stock depletion (Kell *et al.* 2005). Other sources of uncertainty including implementation error (owing to lags in management response)–raising fishing mortality while stocks are declining–would also promote further depletion, thereby posing a greater risk of stock collapse (Kell *et al.* 2005). Although evaluating strategies to lower this risk is beyond the scope of our study, imposing a ceiling on exploitation rate when the stock is declining, for example, may mitigate the probability of overharvest and stock depletion (Gröger *et al.* 2007). Other approaches include suspending stability constraints when stock abundance is above precautionary biological thresholds such as B_{pa}, (Gröger *et al.* 2007). In the NEA cod harvest control rules, the "three-year look ahead" rule, for example, is designed to curtail exploitation rate when stock abundance is above B_{pa} but is declining. When developing harvest policies, we must consider dynamic tradeoffs between maintaining yield stability and minimizing the risk of overharvest (short-term stability vs. long-term sustainability, Kell *et al.* 2005) under uncertainty.

Although large short-term variation in catch is often disfavored by harvesters and seafood processors, patterns in stock variance may provide valuable information about the stock status such as its resilience (Anderson *et al.* 2008). Magnified variance may signal impending internal structural shifts in nature including fished populations (Brock & Carpenter 2010). The analysis of the extensive database on global commercial marine fisheries compiled by the United Nations Food and Agriculture Organization (FAO) suggests that imposed stability in catches can hide early warnings that may help prevent stock collapses–a potential long-term consequence of stabilizing yield (Mullon, Fréon & Cury 2005; Carpenter *et al.* 2015). Stability in living marine resources may, thus, need to be maintained by allowing them to develop resilience (for example, restoring stock structure) rather than imposing apparent stability (Carpenter *et al.* 2015).

The case of the Barents Sea cod-capelin complex illustrates that stability constraints, a widely implemented policy tool, can bring about a counterintuitive outcome; the harvest strategy to constrain short-term yield fluctuation can inadvertently destabilize its stock dynamics when ecosystem productivity varies. Because the model in our study did not account for other sources of uncertainty in ecosystem processes including variable predation pressure (no feedback from cod to capelin), interannual fluctuations in stock abundance and catch under stability constraints are likely conservative estimates. Nevertheless, the findings highlight broader implications of structural uncertainty when designing and analyzing harvest strategies for ecologically connected stocks. Constraining fluctuations of such stocks without accounting for variability in key ecosystem processes–common in many single-species-based assessments–may underestimate the risk of stock depletion and possible collapse (Gårdmark *et al.* 2013). Adapting ecosystem-based approaches (such as use of models of intermediate complexity for ecosystem, Plagányi *et al.* 2014) when evaluating management strategies, as

demonstrated here, will safeguard against such a risk and help sustainably manage valuable living marine resources in increasingly variable oceans (Gårdmark *et al*. 2013).

AUTHORS CONTRIBUTIONS

AAF and DH designed the study. AAF develop the model and ran simulations. DG, AAF, DH, BB, YK, and HG analyzed the model outputs. DG, AAF, DH, BB, YK, and HG wrote and edited the manuscript.

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DATA AVAILABILITY STATEMENT

All survey and catch data used for model development are available at the International Council for the Exploration of the Sea 2010 Arctic Fisheries Working Group Report (https://www.ices.dk/sites/pub/Publication%20Reports/Forms/DispForm.aspx?ID=17227).

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Tables

Table 1. Northeast Arctic (NEA) cod stock status under scenarios of varying levels of catch (TAC) stability constraints. TSB indicates total stock biomass (age 3+); and SSB indicates spawning stock biomass.

		stability constraints in TAC							
stock status	baseline	50%	40%	30%	25%	20%	15%	10%	5%
TSB (million tonnes)	2.27	2.25	2.30	2.25	2.37	2.56	2.78	2.99	3.17
SSB (million tonnes)	1.08	1.07	1.09	1.06	1.13	1.24	1.38	1.49	1.63
catch (thousand tonnes)	684.1	678.5	691.1	667.7	701.5	752.7	805.0	836.2	800.5
recruits (millions)	700.4	690.2	704.7	680.4	707.8	733.9	743.5	764.1	755.2

Figures

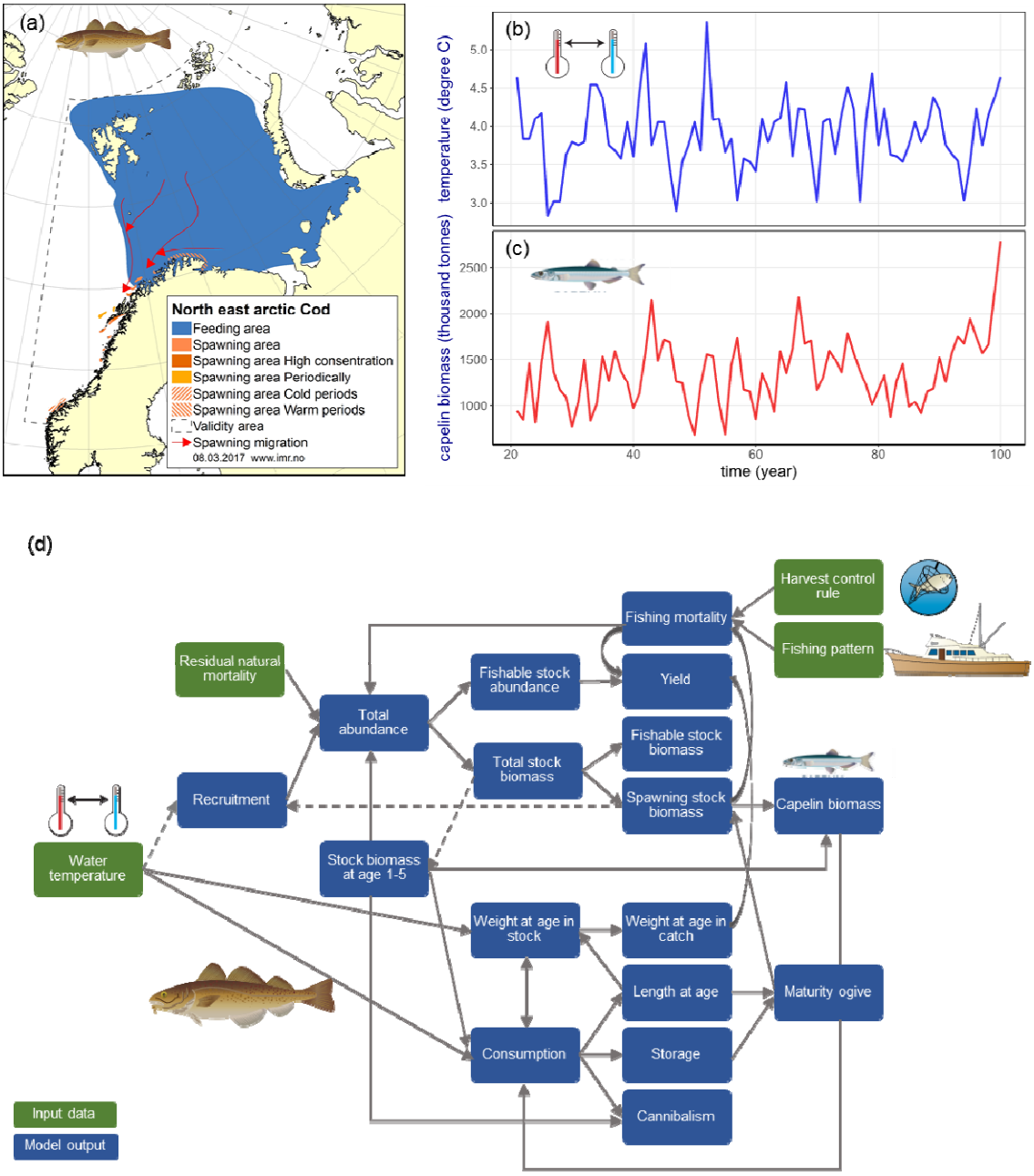


Figure 1. a) Schematic diagram of the Northeast Arctic (NEA) cod–capelin STOCOBAR model structure, b) NEA cod distribution in the Barents Sea, c) modeled ocean temperature (˚C), and d) modeled capelin biomass (1000 tonnes). Artwork: Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

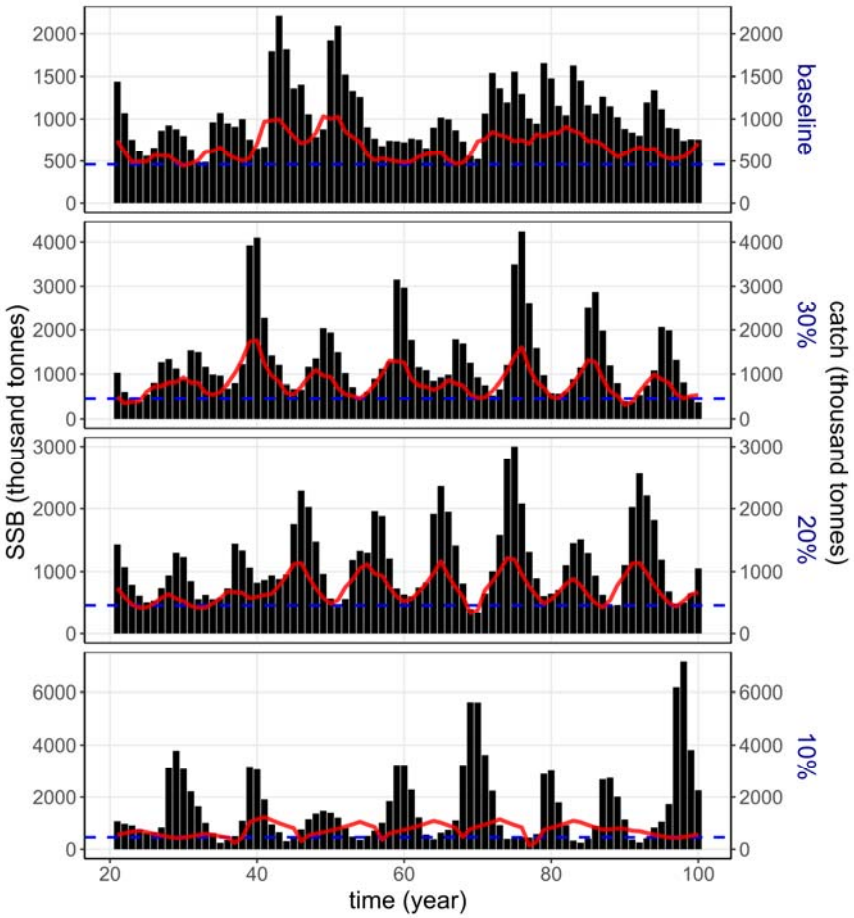
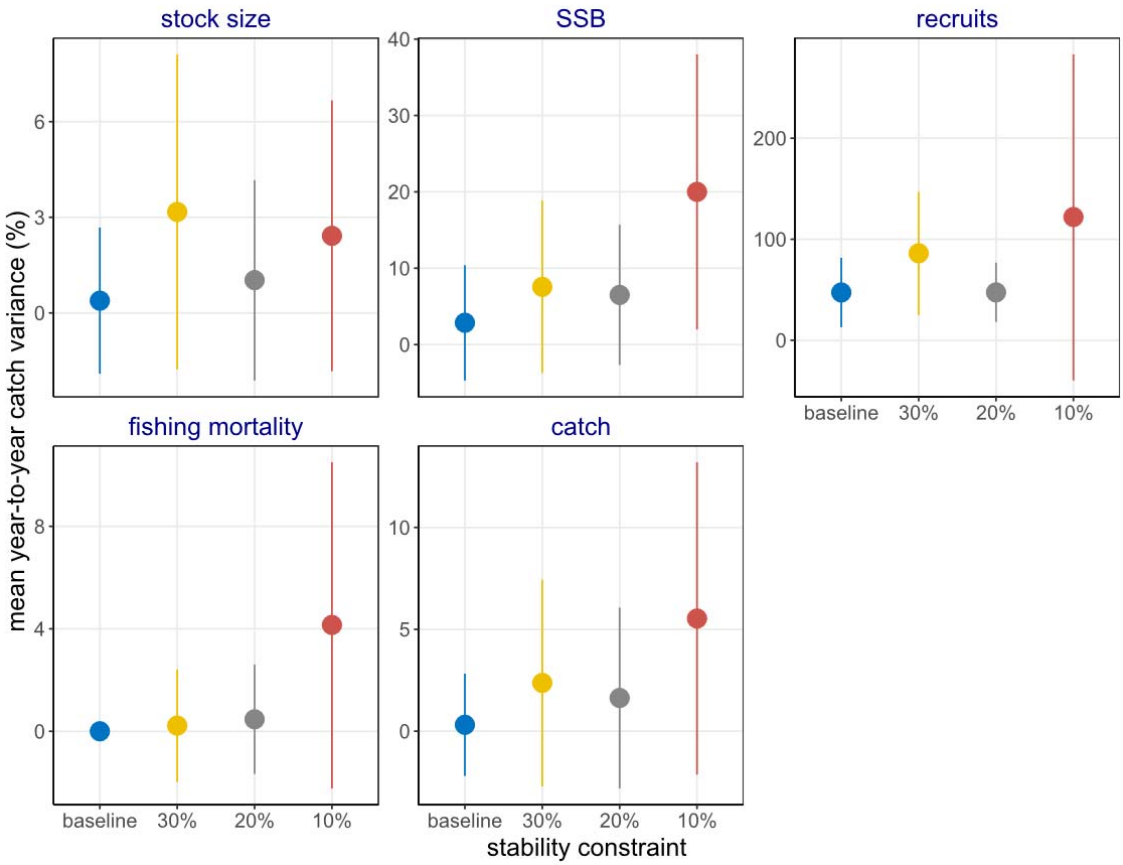


Figure 2. Time series (year 21 to 100) of spawning stock biomass (SSB, black vertical bars) and catch (red solid lines) of the simulated Northeast Arctic (NEA) cod stock under constraint scenario a) no catch constraint, b) ±30% constraint, c) ±20% constraint, and d) ±10% constraint. Blue horizontal dashed lines indicate B_{pa} (= 460 thousand tonnes).


stock size
SSB
recruits
fishing mortality
catch
mean year-to-year catch variance (%)
stability constraint
baseline
30%
20%
10%

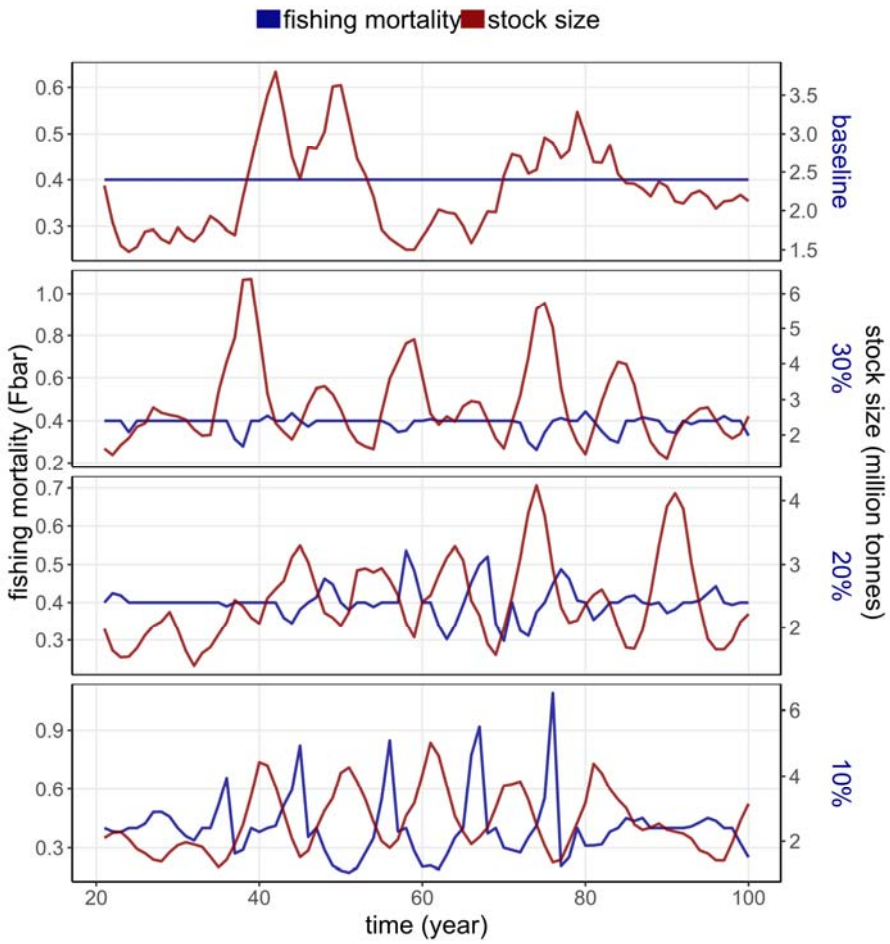


Figure 4. Time series (year 21 to 100) of harvestable (3+)/total stock size and mean fishing mortality (F_{bar}) of Northeast Arctic (NEA) cod under ±0 (baseline), 10%, 20%, and 30% catch constraints.

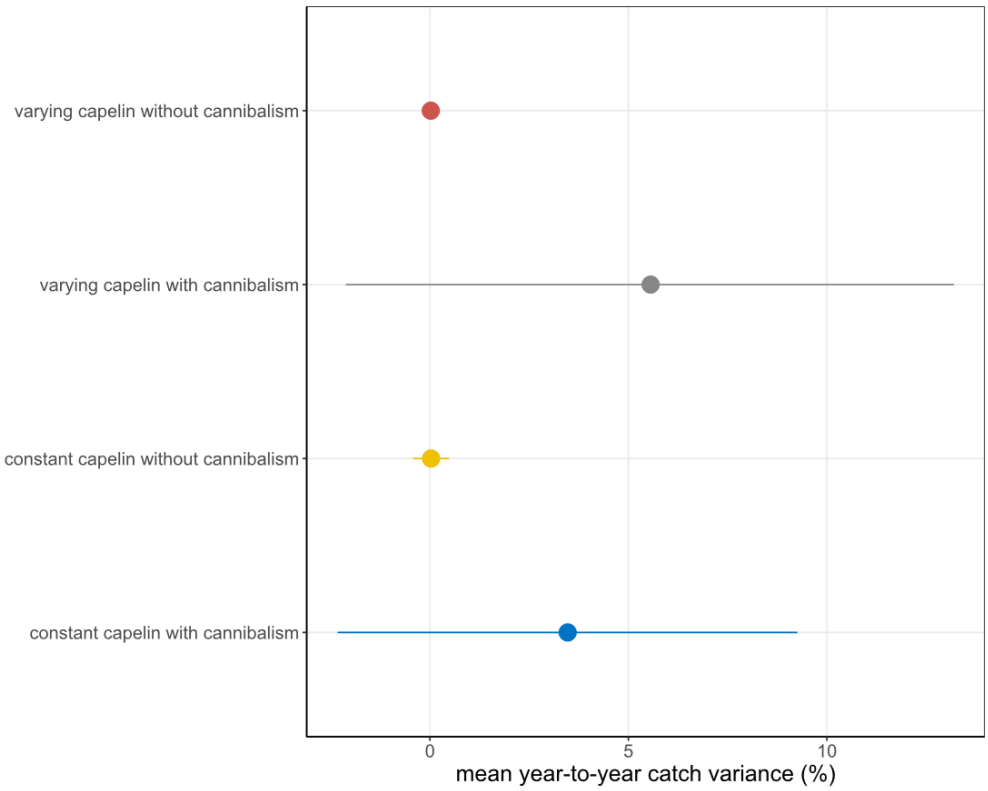


Figure 5. Mean year-to-year catch variance (%) of Northeast Arctic (NEA) cod under a ±10% catch constraint under 1) constant capelin biomass without cod cannibalism, 2) constant capelin biomass with cod cannibalism, 3) varying capelin biomass without cod cannibalism, and 4) varying capelin biomass with cod cannibalism. Error bars indicate 95% confidence intervals (among-year variation).

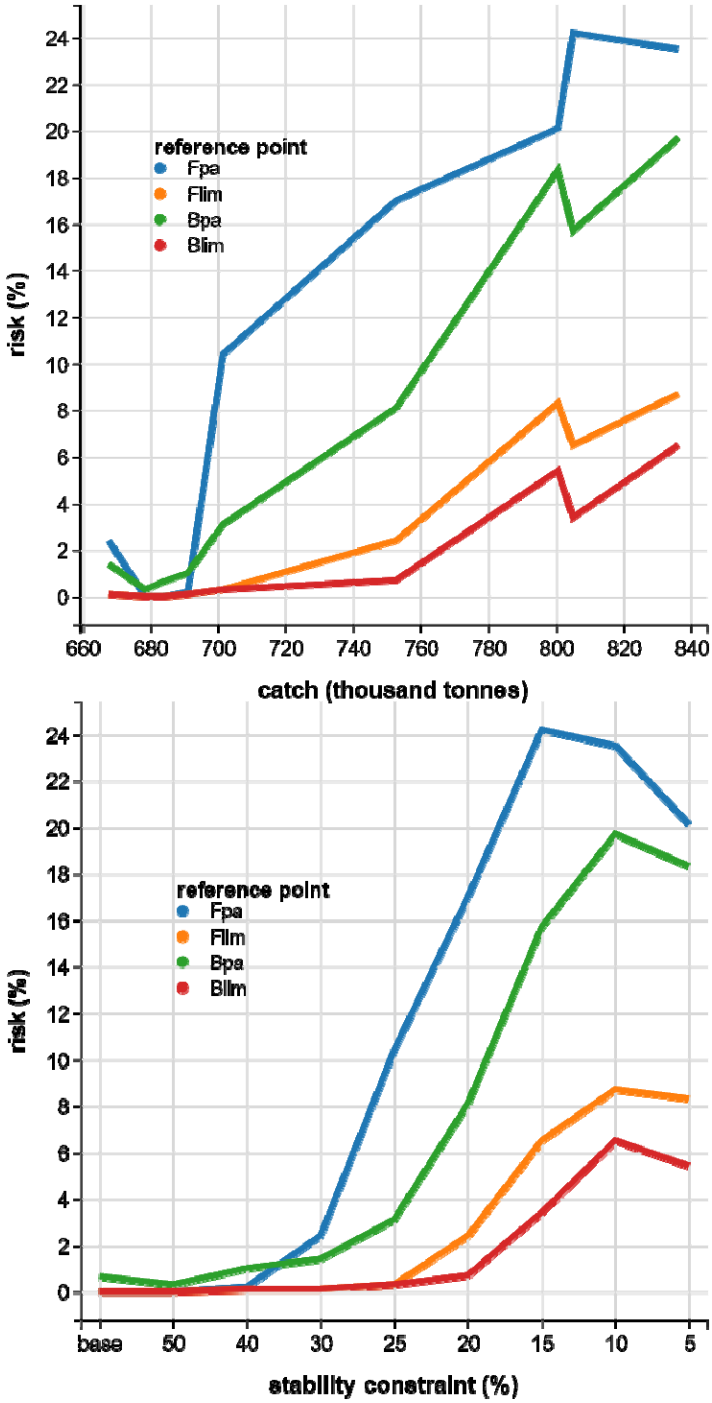


Figure 6. Stock performance against reference points (F_{pa}, F_{lim}, B_{pa}, and B_{lim}) and catch quotas for Northeast Arctic (NEA) cod under varying catch stability constraint (±CV%) scenarios. a) the relationship between catch and the risk (the probability of exceeding the reference points), and b) the risk for varying catch stability constraint. Estimates for the references points for the NEA cod stock are derived from ICES (2003). F_{pa} = 0.40; F_{lim} = 0.74; B_{pa} = 460 thousand tonnes; B_{lim} = 220 thousand tonnes.