

Tradeoffs of managing cod as a sustainable resource in fluctuating environments

DAISUKE GOTO ,^{1,3,4} ANATOLY A. FILIN,² DANIEL HOWELL,¹ BJARTE BOGSTAD,¹ YURY KOVALEV,² AND HARALD GJØSÆTER¹

¹*Institute of Marine Research, P.O. Box 1870, Nordnes, 5817 Bergen, Norway*

²*Polar Branch of the Federal State Budget Scientific Institution, Russian Federal Research Institute of Fisheries and Oceanography ("PINRO" named after N.M. Knipovich), Akademik Knipovich Street 6, Murmansk 183038 Russia*

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Abstract. Sustainable human exploitation of living marine resources stems from a delicate balance between yield stability and population persistence to achieve socioeconomic and conservation goals. But our imperfect knowledge of how oceanic oscillations regulate temporal variation in an exploited species can obscure the risk of missing management targets. We illustrate how applying a management policy to suppress fluctuations in fishery yield in variable environments (prey density and regional climate) can present unintended outcomes in harvested predators and the sustainability of harvesting. Using Atlantic cod (*Gadus morhua*, an apex predatory fish) in the Barents Sea as a case study we simulate age-structured population and harvest dynamics through time-varying, density-dependent and density-independent processes with a stochastic, process-based model informed by 27-year monitoring data. In this model, capelin (*Mallotus villosus*, a pelagic forage fish), a primary prey of cod, fluctuations modulate the strength of density-dependent regulation primarily through cannibalistic pressure on juvenile cod survival; sea temperature fluctuations modulate thermal regulation of cod feeding, growth, maturation, and reproduction. We first explore how capelin and temperature fluctuations filtered through cod intrinsic dynamics modify catch stability and then evaluate how management to suppress short-term variability in catch targets alters overharvest risk. Analyses revealed that suppressing year-to-year catch variability impedes management responses to adjust fishing pressure, which becomes progressively out of sync with variations in cod abundance. This asynchrony becomes amplified in fluctuating environments, magnifying the amplitudes of both fishing pressure and cod abundance and then intensifying the density-dependent regulation of juvenile survival through cannibalism. Although these transient dynamics theoretically give higher average catches, emergent, quasicyclic behaviors of the population would increase long-term yield variability and elevate overharvest risk. Management strategies that overlook the interplay of extrinsic (fishing and environment) and intrinsic (life history and demography) fluctuations thus can inadvertently destabilize fish stocks, thereby jeopardizing the sustainability of harvesting. These policy implications underscore the value of ecosystem approaches to designing management measures to sustainably harvest ecologically connected resources while achieving socioeconomic security.

Key words: *cannibalism; climate change; cohort resonance; early life history; ecosystem-based management; food web; forage fish; population regulation; recruitment dynamics; stock assessment; structural uncertainty; wavelet analysis.*

INTRODUCTION

Fluctuations in wild animal populations can pose myriad socioeconomic and conservation challenges in sustainably managing human exploitation of living

marine resources (Lindgren et al. 2013). Historical records tell us that most harvested populations are far from steady state (Halley and Stergiou 2005). An analysis on more than 200 fish stocks assessed worldwide for example has revealed that nearly three-quarters displayed quasiperiodic variability in productivity (Vert-pre et al. 2013). Such fluctuations may arise from extrinsic forces that prompt life-history events (like reproduction) including climate variability (Cury et al. 2008). Oscillations in these extrinsic forces can amplify or dampen fluctuations in vital rates of a harvested population (Lindgren et al. 2013). Because of covarying responses in

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³Present address: Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Stångholmsvägen 2, Drottningholm, SE-178 93 Sweden

⁴E-mail: daisuke.goto@slu.se

vital rates to environmental variability, however, population fluctuations may not necessarily track environmental signals (Hsieh et al. 2005).

The variability in environmental forcing is filtered through intrinsic processes over ages (or life stages) and may emerge as cyclic behavior in age (or stage)-structured populations (Bjørnstad and Nisbet 2004). For marine populations, large between-year fluctuations often emerge in early life stages; variability in early environments in the sea propagates through life-history processes (Cushing 1990). Density-dependent intercohort and intracohort interactions, such as cannibalism, can generate transient cyclic or quasicyclic patterns in a stochastic environment (Claessen and De Roos 2004). Furthermore, harvested populations that experience persistent, selective reductions in adult survival, which can truncate age structure, may display magnified amplitudes in population fluctuation (Anderson et al. 2008). Past research instructs us that the density-dependent interplay of intrinsic and extrinsic processes can shape these patterns and is likely to be a key contributor to the population variability of many exploited fish species in nature (Minto and Myers 2008, Shelton and Mangel 2011).

Attenuation or amplification of population variability can further resonate through complex interactions among ecologically connected populations to modulate the productivity of a harvested predator (Barraquand 2017). The population cycles of one or more prey in variable environments for example can interactively attenuate or amplify the fluctuations of various life stages of the predator (Barraquand et al. 2017). The stochasticity of physical environments filtered through these processes thus may emerge as complex, nonlinear patterns in harvested predator dynamics (Rouyer et al. 2012), posing a host of challenges in designing and evaluating management measures (Essington and Sanchirico 2018).

In commercial exploitation, stable yields can provide predictability to harvesters and seafood processors, thereby contributing to food, nutrition, and employment security in fishing nations (Garcia and Rosenberg 2010). Resource managers, however, need to balance tradeoffs between maintaining the abundance of an exploited species above a threshold that prevents overharvest and suppressing short-term (here periods of two to four years (yr) as relevant timescales) yield fluctuations to achieve socioeconomic goals (Kell 2006, Carpenter et al. 2015). One such control measure is to set fixed bounds for year-to-year relative change in catch targets; this measure is widely applied in the management of marine fish stocks including high-value species like Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*) (ICES 2019b). The efficacy of yield stability control (also known as stability or catch constraint) applied to stochastic populations is, however, equivocal. This tool can attenuate, magnify, and have little effect on yield variability depending on stock status, life history, and

management cycle, as demonstrated for more than a dozen Northeast Atlantic fish stocks including apex predators like cod, haddock (*Melanogrammus aeglefinus*), and saithe (*Pollachius virens*) (Kell et al. 2005a, 2006, ICES 2019c).

Extrinsic forces such as variable environments may further sway the performance of yield-stabilizing strategies (Walters 1975, Roel and O'Brien 2004). But most analyses evaluate the harvest measure without fully accounting for the dynamic interplay of environmental and demographic fluctuations (ICES 2019b). Mechanisms underlying the variable performance of the amplitude-dampening policy thus remain elusive, with unknown consequences for population persistence and management.

Here we illustrate how applying yield stability control modulates the cyclicity (amplitude and period) of harvested predator dynamics, which in turn redefines levels of sustainable harvest when accounting for stochastically fluctuating environments, using Atlantic cod as a case study. The productivity of cod, a demersal (bottom-water) predatory fish intensely harvested in the North Atlantic (Frank et al. 2016), fluctuates with variability in both density-dependent and -independent processes during early life stages (Dingsør et al. 2007). Density-independent thermal regulation of early life stages contributes to variability in cod recruitment (Bogstad et al. 2013). These processes further interact with nonlinear density feedbacks in cod dynamics mediated through interspecific and intraspecific interactions (Dingsør et al. 2007). Delayed density-dependent regulation of juvenile survival through cannibalism in particular is tightly coupled with the fluctuations of pelagic forage fishes, a primary food source of adult cod, like capelin (*Mallotus villosus*), sprat (*Sprattus sprattus*), and herring (Link et al. 2009). Adult cod consume the young more during years of low prey densities, thereby weakening the strength of year classes (Durant et al. 2008). Due to migration driven by ocean conditions, pelagic fish fluctuations also reflect changes in climate-forced ecosystem processes, including systemwide shifts in ice phenology, thermal regimes, and plankton productivity (Carscadden and Frank 2001). The dynamic predator-prey interactions coupled with large-scale oceanic processes, and combined with intense fishing pressure (Frank et al. 2016), may contribute to fluctuations in cod fishery yields (Lilly et al. 2008).

Using a stochastic, process-based model informed by system-specific information from the Barents Sea we explore how variability in extrinsic forcing is propagated through the intrinsic dynamics of an age-structured population by explicitly simulating the key mechanisms that can regulate cod productivity—the interplay of cannibalism, capelin density, and climate variability—under a given harvest regime. Specifically, we ask: (1) *how do climatic oscillation and capelin fluctuation filtered through cod life-history processes affect cod yield stability?* and (2) *how does applying a measure intended to suppress yield*

variability in variable environments change the potential to achieve management targets? In effect, our work aimed to better understand underlying causes of yield fluctuations by adopting an ecosystem approach to inform sustainable use of fish stocks while achieving socioeconomic goals.

METHODS

Study system

The Barents Sea cod–capelin complex is among the few co-managed stocks in the North Atlantic (Gjøsæter and Tjelmeland 2012). Barents Sea cod (also known as North-east Arctic cod), distributed over the Barents and its adjacent areas (Fig. 1a), is the world’s largest cod stock supporting fisheries of two nations: Norway and Russia (Kjesbu et al. 2014). The fishery dates back to the period when the northern coasts of these nations were populated after the end of the last ice age (~12,000 yr ago), with a commercial fishery dating back at least half a millennium (Øiestad 1994). An international industrial trawl fishery in the Barents Sea developed in the early twentieth century and total catches peaked at more than 1.2 million tons (t) during 1955–1975 (ICES 2019a). Following the establishment of 200-mile economic zones in the late 1970s the fishery by Norway and Russia dominated (ICES 2019a). In the early 2000s the Joint Norwegian–Russian Fisheries Commission, a regional management body, adopted a harvest strategy that was jointly developed by managers and the International Council for Exploration of the Sea (ICES 2019a). This harvest strategy sets target exploitation rate with precautionary measures, which account for imperfect knowledge about the stock, while achieving near-term yield stability by suppressing year-to-year variability in catch quotas. These harvest measures, along with strong year classes during 2004–2006, allowed the population to balloon again with the quota reaching one million t in 2014—the highest in more than three decades (Kjesbu et al. 2014).

Capelin, a pelagic, schooling fish that rarely reaches more than 20 cm and lives no more than five years, is the major forage species supporting apex predators in the Barents (Gjøsæter 1998). Its biomass, estimated by acoustic methods, has reached up to seven million t in the 1970s and 1990s (Gjøsæter 1998). Capelin feed on meso- and macro-zooplankton in the northern Barents, but migrate to the northern coasts of Norway and Russia to spawn in spring. Although many piscivores in the region feed on capelin, cod is by far their primary predator, consuming more than three million t per year (Dolgov 2002). Amplified year-to-year fluctuations in capelin in the 1980s and 1990s also shaped cod biomass rebuilding patterns: for example, cod cannibalism peaked after capelin collapses (Yaragina and Kovalev 2018). The collapses, particularly the first one, propagated further through the rest of the food web (Gjøsæter and Bogstad 2009).

Modeling cod dynamics

To evaluate how the cod population responds to different harvest measures under varying capelin production and climate, we used a stochastic, food-web model (“Stock of Cod in the Barents Sea” or StoCoBar), which had been previously developed and applied in various forms in peer-reviewed studies and stock assessments (Howell et al. 2013 and references therein). This model primarily hinges on energetics principles to capture age-structured dynamics through individual-level processes in dynamic environments (Fig. 1d). The model is grounded in observational data and is designed to project cod dynamics and evaluate management strategies by accounting for variability in ecosystem processes. In the following we describe: (1) model structure and parameterization, (2) harvest management measures, (3) key model assumptions on environmental forces, and (4) simulation scenarios and analyses.

Food-web model

Model structure.—The model simulates cod dynamics (1- to 15-year-olds) through life-history processes at yearly time steps: time-varying reproduction, mortality (fishing, cannibalism, and other natural causes), feeding, growth, and maturation (Fig. 1d). We assume that annual reproduction, defined by survival of 1-year-olds (recruitment), depends on adult (female only) abundance (spawner stock biomass, SSB, t) and sea temperature (°C), and then on cannibalism and capelin abundance (Fig. 1d). SSB is computed by multiplying age-specific adult numbers by mass (kg). The model simulates cod recruitment with a modified Ricker model, which is a function of SSB and sea temperature (Table 1: Eq. 1; Hilborn and Walters 2013). We used the model previously parameterized through an iterative, forward-simulation procedure described in Howell et al. (2013).

We assume that some fish die from cannibalism during the first three years of life and that fishing (by a single aggregate fleet with time-invariant, age-specific gear selectivity) removes 3- to 15-year-olds (Table 1: Eq. 2a–d). The model mechanistically simulates time-varying cannibalism through food consumption rates (kg/yr, Fig. 1d, Table 1: 3a–e), assuming that mortality rates by other natural causes (like starvation) are constant (M , Table 2). The model simulates consumption by cod using temperature-, prey-, and cod density-dependent functions (Table 1: Eq. 3a–e). We used capelin as a primary food source for cod with all other prey commonly found in cod stomachs (including young haddock and herring, polar cod [*Boreogadus saida*], shrimp [*Pandalus borealis*], and krill [Euphausiidae]) being aggregated as other food. In effect, capelin biomass acts as a proxy for cod carrying capacity, representing good and poor years of habitat conditions that regulate cod population growth (Gjøsæter 1998). The consumption rates of only 3- to 7-year-olds directly depend on capelin biomass (Table 1: Eq. 3d). Although older cod

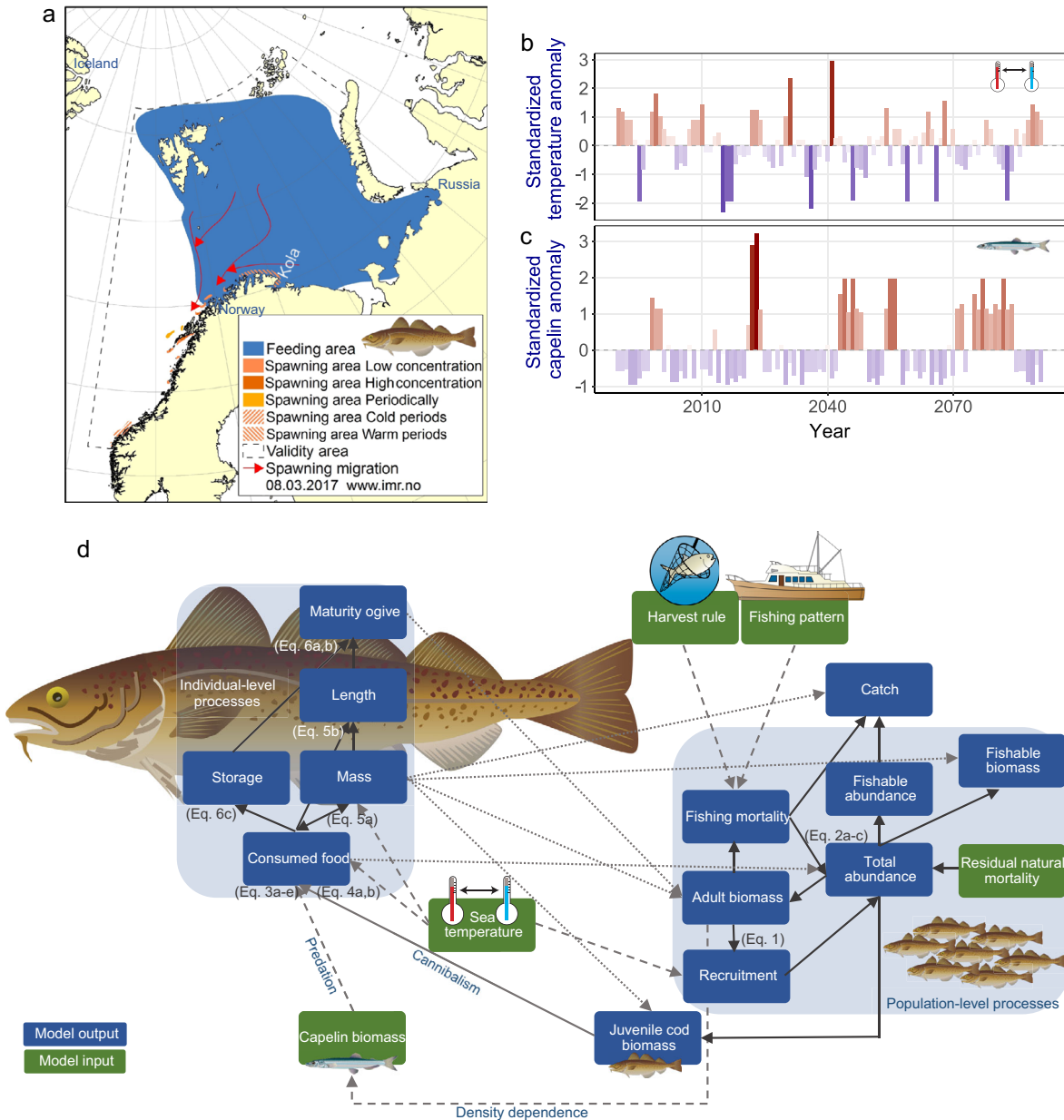


FIG. 1. Study system and the model. (a) Cod distribution in the Barents Sea and adjacent areas. Spawning areas are defined based on spawner abundance and/or the frequency of spawning: annual spawning with low and high concentrations (orange and red, respectively) and periodic spawning, cold periods in the north (left diagonal lines) and warm periods in the north (right diagonal lines) (Sundby and Nakken 2008). (b) Example of simulated sea temperatures (standardized anomalies) in the model based on observed annual mean temperatures in the Kola section (70°3'N–72°30'N at 33°30'E). Standardized anomalies are computed by subtracting modeled annual temperatures from the mean and dividing by the standard deviation. (c) Example of simulated capelin production (standardized anomalies) in the model based on observed capelin biomass in the Barents Sea. Standardized anomalies are computed by subtracting modeled annual capelin biomass from the mean and dividing by the standard deviation. (d) Schematic diagram of the model structure of StoCoBar, a stochastic, food-web model. Boxes indicate state variables, solid lines indicate flows of information within individual-level or population-level processes, dotted lines indicate flows of information from individual-level to population-level processes, dashed lines indicate flows of information between model input and state variables, and equation (Eq) numbers refer to the equations in Table 1.

also feed on capelin, their consumption rates are assumed independent of capelin biomass (Table 1: Eq. 3c) because older cod can migrate and switch to other prey when capelin biomass declines (Kjesbu et al. 2014) (Appendix S1:

Fig. S1). Realized diet composition (in proportion) depends on prey biomass (t) and time-invariant suitability indices (Table 1: Eq. 4a). Based on model fitting we fixed maximum mortality rates by cannibalism for one- to

TABLE 1. The main equations used in the Barents Sea food-web model (StoCoBar) and cod management model.

| Description | Equation | Eq. no. |
|----------------------------|---|---------|
| Population dynamics | | |
| Recruitment | $\log\left(\frac{R_y}{(\overline{\text{SSB}})_y}\right) = \alpha_1 + \alpha_2(\text{SSB})_y + \alpha_3 T_y$ | (1) |
| Age 2–3 | $N_{a,y+1} = N_{a-1,y} e^{-M} P_{a-1,y}$ | (2a) |
| Age 4 | $N_{4,y+1} = N_{3,y} e^{-(F_{3,y}+M)} - P_{3,y}$ | (2b) |
| Age 5–15 | $N_{a,y+1} = N_{a-1,y} e^{-(F_{a-1,y}+M)}$ | (2c) |
| Predation mortality | | |
| (age 1–3) | $P_{a,y} = \frac{\sum_{a=5}^{15} (\text{FC})_{a,y} (\text{DC})_{\text{cod},a,y}}{W_{a,y}}$ | (2d) |
| Feeding | $(\text{FC})_{a,y} = \tau_{a,y} (\text{FC})_{\text{max},a,y}$ | (3a) |
| Age 1–2 and 8–15 | $\tau_{a,y} = \beta_1 e^{-\beta_2 \frac{B_{a,y}}{\beta_3}}$ | (3b) |
| Age 3–7 | $\tau_{a,y} = 0.5 + \frac{0.5(\ln(1+\lambda_{a,y}) - \beta_4)}{\ln(1+\lambda_{a,y}) + \beta_4 + \beta_5}$ | (3c) |
| | $\lambda_{\text{prey},a,y} = \frac{(\text{DC})_{\text{prey},a,y} B_{\text{prey},a}(\omega_a (\text{DC})_{\text{prey},a,y} W_{a,y} \overline{N}_{a,y})}{\sum_{a=2}^{15} \omega_a (\text{DC})_{\text{prey},a,y} W_{a,y} N_{a,y}}$ | (3d) |
| | $(\text{FC})_{\text{max},a,y} = \gamma_1 e^{\gamma_2 T_y - 0.000112 T_y^3} W_{a,y}^{\gamma_3}$ | (3e) |
| Diet composition | | |
| | $(\text{DC})_{i,a,y} = (1 - (\text{DC})_{\text{other},a,y}) \frac{B_{\text{prey},i,y} S_{i,a}}{\varphi_{a,y}}$, where $\varphi_{a,y} = \sum_{i=1}^m B_{\text{prey},i,y} S_{i,a}$ | (4a) |
| | $(\text{DC})_{\text{other},a,y} = (\text{DC})_{\text{other min},a} + (1 - (\text{DC})_{\text{other min},a}) \frac{\overline{\varphi}_a}{\varphi_a + \rho_a \varphi_{a,y}}$ | (4b) |
| Growth | | |
| | $\Delta W_{a,y} = 1.11 \frac{(\text{FC})_{\text{keal},a,y}}{\delta_1 W_{a,y}^{0.15}} - 2.29 W_{a,y}^{\delta_2} e^{0.081 T_y + 0.002128 L_{a,y}}$ | (5a) |
| | $\Delta L_{a,y} = \left(\frac{(\text{FC})_{\text{keal},a,y}}{\mu_1 W_{a,y}^{\mu_2}} - \mu_3 W_{a,y}^{0.833} e^{0.081 T_y + 0.002128 L_{a,y}} \right) 0.333$ | (5b) |
| Maturation | | |
| Age 4–5 | $D_{a,y} = \frac{1}{1 + e^{\epsilon_1 L_{a,y} + \epsilon_2}}$ | (6a) |
| Age 6–9 | $D_{a,y} = \frac{1}{1 + e^{\epsilon_1 L_{a,y} + \epsilon_3 F_{\text{mat},a-1,y-1} + \epsilon_2}}$ | (6b) |
| | $\text{Fat}_{a,y} = \kappa_1 e^{-\kappa_2 (\text{FC})'_{a,y}}$, where $(\text{FC})'_{a,y} = \frac{(\text{FC})_{a,y}}{\Delta W_{a,y}}$ | (6c) |
| Target exploitation | | |
| | $F_{\text{target},y} = F_{\text{pa}} \frac{(\text{SSB})_y}{B_{\text{pa}}}$ | (7) |
| Catch variability | | |
| | $\text{ICV}_y = \frac{C_{\text{target},y} - C_{\text{target},y-1}}{C_{\text{target},y-1}} \times 100$ | (8) |
| Fishing mortality | | |
| | $F_{a,y} = \frac{F_{\text{target},y}}{F_{5-10,1}} F_{a,1}$ | (9) |

Note: The description of variables and parameters of the equations are given in Table 2.

three-year-olds at 0.9, 0.6, and 0.4 (respectively). The model simulates the proportion of other food using an empirical function fit to historical data on cod stomach content, and cod and capelin biomass (Table 1: Eq. 4b).

To simulate individual growth, the model converts the amount of consumed food (kcal) to changes in body mass and length (cm) using temperature- and cod density-dependent functions (Fig. 1d, Table 1: Eq. 5a,b, Jones 1978). For simplicity we assumed that the energy content of consumed food was time-invariant and estimated through model fitting. The model then uses a length-dependent function to simulate maturation for four- and five-year-olds and a length- and condition-dependent function for six- to nine-year-olds (Fig. 1d, Table 1: Eq. 6a,b). The latter function uses the amount of consumed food relative to growth as a proxy for condition (Fig. 1d, Table 1: Eq. 6c). All one to three-year-olds are immature and all ten- to fifteen-year-olds mature following the assumption adopted in the Arctic Fisheries Working Group stock assessment (ICES 2011).

Parameterization.—We used an integrated approach to parameterizing the submodels: consumption, diet composition, growth, and maturation (Appendix S1: Fig. S1).

This approach uses reconstructed time series of age-specific numbers and fishing mortality rates (Appendix S1: Tables S1, S2) taken from the stock assessment and survey data on prey biomass and sea temperature (ICES 2011) as input to fit the model through the following four-step procedure (Appendix S1: Fig. S1). First, we fitted the model to total stomach content mass data to estimate consumption model (Table 1: Eq. 3a–e) parameters (β_{1-5} , γ_{1-3} , and ω ; Table 2; Appendix S1: Table S5) using a nonlinear least squares (NLS) method (Appendix S1: Fig. S2). Second, we fitted the model to stomach content composition data to estimate diet composition model (Table 1: Eq. 4a, b) parameters ($(\text{DC})_{\text{other min}}$ and ρ ; Table 2) including age-specific suitability index for each prey (S ; Table 2; Appendix S1: Table S6) using a correlation maximization method (Appendix S1: Fig. S3). The first two steps were performed iteratively (Appendix S1: Fig. S1) until the model captured the observed patterns. Third, we fitted the model to cod mass data (Appendix S1: Table S3) to estimate growth model (in mass and length; Table 1: Eq. 5a, b) parameters (δ_{1-2} and μ_{1-3} ; Table 2; Appendix S1: Table S5) using NLS (Appendix S1: Fig. S4a). Next, we fitted the model to maturity data (Appendix S1: Table S4) to estimate maturation model (Table 1: Eq. 6a–c)

TABLE 2. List of the variables and parameters in the Barents Sea food-web model (StoCoBar) and cod management model.

| Variable/parameter | Description | Source |
|---|--|---|
| $N_{a,y}$ | a -year-old cod number in year y | ICES (2011) for historical (1984–2010) estimates |
| $F_{a,y}$ | a -year-old cod fishing mortality rate in year y | ICES (2011) for historical (1984–2010) estimates |
| M | Residual natural mortality rate | 0.0 for one and two-year-olds and 0.2 for three-year-olds and older |
| $P_{a,y}$ | a -year-old cod number eaten by adults in year y | |
| R_y | One-year-old cod number recruited in year y | |
| SSB_y | Cod spawner biomass (kg) in year y | |
| T_y | Annual mean water temperature at 0–200 m in the Kola section | PINRO database |
| $\alpha_1, \alpha_2, \alpha_3$ | Cod recruitment model parameters estimated through model fitting | Howell et al. (2013) |
| $FC_{a,y}$ | Amount of consumed food (kg) by a -year-old cod in year y | |
| $\tau_{a,y}$ | Proportion of maximum food consumption by a -year-old cod in year y | |
| $FC_{\max,a,y}$ | Maximum food consumption by a -year-old cod in year y | |
| $B_{a,y}$ | a -year-old cod biomass (kg) in year y | |
| $\lambda_{a,y}$ | Food availability index for a -year-old cod in year y | |
| $\beta_1, \beta_2, \beta_3, \beta_4, \beta_5$ | Cod feeding model parameters estimated through model fitting | This study |
| $W_{a,y}$ | a -year-old cod mass (g) in year y | ICES (2011) for historical (1984–2010) estimates |
| ω | Food availability index parameter | This study |
| $\gamma_1, \gamma_2, \gamma_3$ | Cod maximum consumption parameters estimated through model fitting | This study |
| $DC_{i,a,y}$ | Proportion of prey i in diet of a -year-old cod in year y | |
| $DC_{\text{other},a,y}$ | Proportion of other prey aggregate in diet of a -year-old cod in year y | |
| $B_{\text{prey},i,y}$ | Biomass of prey i in the environment in year y | PINRO and IMR databases |
| $S_{i,a}$ | Suitability index of prey i for a -year-old cod | This study |
| $\phi_{a,y}$ | Food availability index for a -year-old cod in year y | |
| $DC_{\text{othermin},a}$ | Minimum proportion of other prey aggregate in diet of a -year-old cod | This study |
| $\bar{\phi}_a$ | Long-term mean food availability index for a -year-old cod | Howell et al. (2013) |
| ρ_a | Minimum other prey model parameter for a -year-old cod estimated through model fitting | This study |
| $\Delta W_{a,y}$ | a -year-old cod growth in mass (g) in year y | |
| $FC_{\text{kacl},a,y}$ | Amount of consumed energy (kcal) by a -year-old cod in year y , which is converted from $FC_{a,y}$ using conversion factors in Appendix S1: Table S7 | |
| $L_{a,y}$ | a -year-old cod length (cm) in year y | IMR and PINRO databases |
| δ_1, δ_2 | Cod growth (in mass) model parameters estimated through model fitting | This study |
| $\Delta L_{a,y}$ | a -year-old cod growth in length (cm) in year y | |
| μ_1, μ_2, μ_3 | Cod growth (in length) model parameters estimated through model fitting | This study |
| $Fat_{a,y}$ | Condition index for a -year-old cod in year y | |
| $FC'_{a,y}$ | Consumed food relative to growth in mass for a -year-old cod in year y | |
| κ_1, κ_2 | Cod condition index parameters estimated through model fitting | This study |
| $D_{a,y}$ | Proportion of adults in a -year-old cod in year y | |
| $\epsilon_1, \epsilon_2, \epsilon_3$ | Cod maturation model parameters estimated through model fitting | This study |
| $F_{5-10,1}$ | Mean fishing mortality rate of five to ten-year-olds (the dominant age classes in observed catches) in 1990 (0.274) | ICES (2011) |
| $F_{a,1}$ | Fishing mortality rate of a -year-olds in 1990 (Appendix S1: Table S2) | ICES (2011) |
| $F_{5-10,y}$ | Mean fishing mortality rate in year y | |

parameters (κ_{1-2} and ε_{1-3} ; Table 2; Appendix S1: Table S5) using NLS (Appendix S1: Fig. S4b). All tuning data used in this procedure had been collected during 1984–2004 (in which all data were consistently available).

Cod management measures

We simulated dynamic cod mortality by fishing using a model based on the current harvest rule set for Barents Sea cod (with some simplifications, see Appendix S1, ICES 2016) and evaluated cod population and yield variability under alternative harvest measures. Under this harvest rule, target exploitation rate (F_{target} , yr⁻¹) is set to 0.40 to project annual catch target (C_{target} , t) when the SSB remains above 460,000 t. The C_{target} is computed by multiplying harvestable (three-year-olds and older) biomass (stock size, t) by $\exp(-F_{\text{target}})$. These reference values of the exploitation rate and SSB (0.40 and 460,000) are designed to take precautionary measures (termed F_{pa} and B_{pa} , respectively) to prevent overexploitation by accounting for uncertainty in population and harvest dynamics (Kell et al. 2005a) and have been previously selected through simulation-based evaluation (ICES 2016). When the SSB in year y (SSB_y) falls below B_{pa} , F_{target} in year y ($F_{\text{target},y}$) is adjusted to F_{pa} scaled to the proportion of SSB_y relative to B_{pa} (Table 1: Eq. 7). Also, the harvest rule has a policy tool to suppress between-year variability in C_{target} (yield stability control) within $\pm 10\%$ (prior to the latest evaluation, ICES 2016). We computed a relative change in C_{target} from year $y - 1$ to y (interannual catch variability, ICV_y , %, Table 1: Eq. 8). In simulations, when ICV_y exceeds the set proportion, the algorithm searches for $F_{\text{target},y}$ until it finds the largest value that does not exceed the bounds set by the stability control. But the precautionary principle also applies to this policy. The stability control is applied only when SSB_y equals to or exceeds B_{pa} ; this can result in asymmetrical applications (more frequent applications in the positive direction). The stability control is not applied in the first year after the recovery period ($\text{SSB}_y \leq B_{\text{pa}}$). Once $F_{\text{target},y}$ is set, fishing mortality rates of a -year-olds in year y ($F_{a,y}$) are computed relative to those in the initial year of simulations (1990 in this study) (Table 1: Eq. 9).

Environmental forcing

Sea temperature.—This study primarily focused on between-year fluctuations because two to four years is the relevant timescale for provisioning tactical advice in fisheries management such as multiannual plans (ICES 2019b). The model uses a stochastically simulated thermal regime that reflects the historical (1950–2017) fluctuation of annual mean temperatures (AMT) in the Kola section (70°30'N–72°30'N at 33°30'E; Fig. 1a), which also roughly represents climate variability in the region (Ingvaldsen et al. 2003). To generate a plausible temperature fluctuation scenario, we first split the AMT data (averaged across 0–200 m) into three groups: cold

(AMT < 3.6°C), moderate (3.6°C ≤ AMT ≤ 4.2°C), and warm (AMT > 4.2°C) years; we determined the threshold values based on the frequency distribution of the historical data. Then, we randomly selected temperatures from these three groups sequentially; the length of each period was randomly set so that the simulated thermal periods (cold, moderate, and warm) would last from one to five years, effectively generating roughly decadal (autocorrelated) oscillations (Fig. 1b).

Capelin production.—We assumed that capelin production (as change in total biomass) depends on previous year's cod and capelin abundance to capture the historical patterns of density-dependent predation and autocorrelation (respectively). Although capelin is targeted for commercial harvest in the system, the model does not simulate this fishery explicitly. We empirically generated a variable production scenario using the historical (1972–2010) biomass data (Appendix S1: Fig. S5) as described in Howell et al. (2013). Briefly, annual capelin biomass was randomly selected with replacement from the dataset twice every year in simulations using empirical functions: one based on cod SSB and another on capelin biomass in the previous year, and then the mean was used as input (Howell et al. 2013). To prevent biologically implausible fluctuations in simulations, we fixed capelin biomass at six million t when projected cod SSB exceeded 800,000 t. With this approach, simulated capelin production stochastically varied among years and replicates (Appendix S1: Fig. S5), generating low-frequency oscillations (Fig. 1c).

Stochasticity in cod recruitment.—To account for process uncertainty in cod productivity, we added noise to simulated recruit numbers (Table 1: Eq. 1). We randomly generated normally distributed deviates, $N(0, \sigma^2)$, where σ is the standard deviation estimated through model fitting using the SSB–recruit historical data as described above (see *Food-web modeling*); this process was independently repeated every year for each replicate in simulations.

Scenarios and simulations

Ecological scenarios.—Although cannibalism was incorporated as a source of juvenile mortality in the latest evaluation of the harvest rules, environmental conditions that may drive cannibalism strength such as capelin density were assumed constant (ICES 2016). We explored how variable environments (capelin production and climate) and cod cannibalism interactively contribute to cod fluctuations and affect the efficacy of yield stability control using different model configurations. We tested the following four configurations under a 10% catch constraint (ICV): (M1) constant capelin biomass (one million t) and varying sea temperature without cannibalism, (M2) varying capelin biomass and temperature without cannibalism, (M3) constant capelin biomass

and varying temperature with cannibalism, and (M4) varying capelin biomass and temperature with cannibalism. In analyzing the ecological scenarios we computed five cod demographic state variables and management targets from model projections: stock size, SSB, juvenile biomass, juvenile survival (defined as three-year-old abundance), and C_{target} .

Stability control scenarios.—To evaluate how suppressing year-to-year fluctuations in C_{target} influences cod population cycles and yield stability in fluctuating environments, we analyzed nine harvest scenarios of limiting ICVs using model configuration M4: no constraint (baseline), $\pm 50\%$, $\pm 40\%$, $\pm 30\%$, $\pm 25\%$, $\pm 20\%$, $\pm 15\%$, $\pm 10\%$, and $\pm 5\%$. In analyzing the harvest scenarios, we computed seven cod demographic state variables and management targets from model projections: stock size, SSB, juvenile biomass, juvenile survival, C_{target} , F_{5-10} , and risk (%). Risk is defined as the probability of SSB falling below the biological limit threshold (B_{lim} , Kell et al. 2005a) in the last 20 yr of simulations (2071–2090). When $\text{SSB} < B_{\text{lim}}$, the reproductive capacity of a population is expected to decline (Kell et al. 2005a); harvest rules with risk $> 5\%$ are considered unacceptable (non-precautionary) for sustainable exploitation. For Barents Sea cod, B_{lim} is set to 220,000 t (ICES 2016).

We initialized simulations with the 1990 estimates of age-specific demographic parameters and fishing mortality rates taken from the stock assessment (ICES 2011) and projected 101-yr (1990–2090) population and harvest dynamics. We disregarded the first 41 yr of model projections (1990–2030) to minimize effects of the initial conditions. We analyzed each scenario based on 25 realizations because exploratory simulations showed convergence in the means and standard deviations of medium and long term (2031–2070 and 2071–2090, respectively) C_{target} and SSB both across replicates and across years after 25 replicates (the coefficients of variation among simulations with different replicate numbers remained < 0.06 ; Appendix S1: Figs. S6, S7). Because this study primarily focused on the implications of suppressing yield fluctuations, we did not account for other sources of uncertainty such as population estimation and implementation errors (we assume that annual yields are equal to C_{target}). We ran 325 simulations in total to evaluate ecological assumptions (models) ($25 \times 4 = 100$ simulations) and harvest scenarios ($25 \times 9 = 225$ simulations).

Wavelet analyses

To explore patterns of variability in projected cod population and yield, we performed wavelet spectral analysis on model outputs from selected scenarios of environmental forces (sea temperature and capelin, model configuration M4) and harvest rules (baseline, 10%, 20%, and 30% constraints). Wavelet spectral analysis is suited for characterizing patterns of variance in nonlinear and non-stationary time series with stochastic

noise (Cazelles et al. 2008) such as transient population dynamics of exploited species. We computed continuous Morlet wavelet power (the square of amplitudes) spectra to transform signals as a function of frequency (periodicity) and time from 1,000 bootstrap simulations (randomized surrogate time series) (Roesch and Schmidbauer 2018). We computed a spectrum for each replicate of projected time series (2031–2090) for the following four cod demographic state variables and management targets: stock size, SSB, juvenile survival, and C_{target} . To evaluate synchronicity between cod population and harvest dynamics, we performed cross-wavelet analysis to test for coherency (covariation in frequency) (Cazelles et al. 2008) between stock size and F_{5-10} time series for each replicate and made inferences based on averages across transformed replicates. We performed all wavelet analyses in R (version 3.6.2, R Development Core Team 2019) with the WaveletComp R package v.1.1 (Roesch and Schmidbauer 2018).

RESULTS

Ecological uncertainty in cod harvest dynamics

Density-dependent cannibalism played a key role in driving non-stationary patterns of cod population and catch fluctuations under yield stability control in simulations (Fig. 2). Without cannibalism, both varying capelin production and sea temperature (M1 and M2) induced low variability in cod (adult and juvenile) biomass (< 0.04 of the CV across years; Appendix S2: Fig. 1a), and ICVs remained $< 2\%$ (the stability control was never triggered; Fig. 2b). These patterns reflect the extrinsic signals filtered through life-history processes such as recruitment and maturation (but without intra-cohort interactions) in age-structured dynamics, as also revealed by wavelet transformation of catch time series (M1: ~ 9 -yr cycles; M2: ~ 12 - and 32-yr cycles; Fig. 2a; Appendix S2: Fig. S3a,b). By contrast, with cannibalism and constant capelin production (M3) added, the CV in cod biomass rose to more than 0.20 (Appendix S2: Fig. 1b), and mean ICV across years rose 2.4-fold (the stability control was applied in $\sim 7\%$ of the projection years, Fig. 2b). Cannibalism in our model filters variability both in extrinsic (capelin and temperature) signals and in intrinsic population dynamics including density-dependent juvenile survival, generating quasicycles in cod biomass and catch (Fig. 2a; Appendix S2: Fig. S1b). Wavelet transformation of catch time series revealed ~ 8.5 -yr cycles, reflecting sea temperature variability augmented by cod intrinsic cycles (Fig. 2a). When combined with varying capelin production (M4), the CVs in adult and juvenile biomass further rose (0.96 and 0.62, respectively; Appendix S2: Fig. 1b), and mean ICV rose nearly 40-fold (Fig. 2a). This amplified variability emerges from frequent, asymmetrical applications (more than 70% of the years) of the stability control (seen as flat lines in Fig. 2b), which disrupted cod population cycles

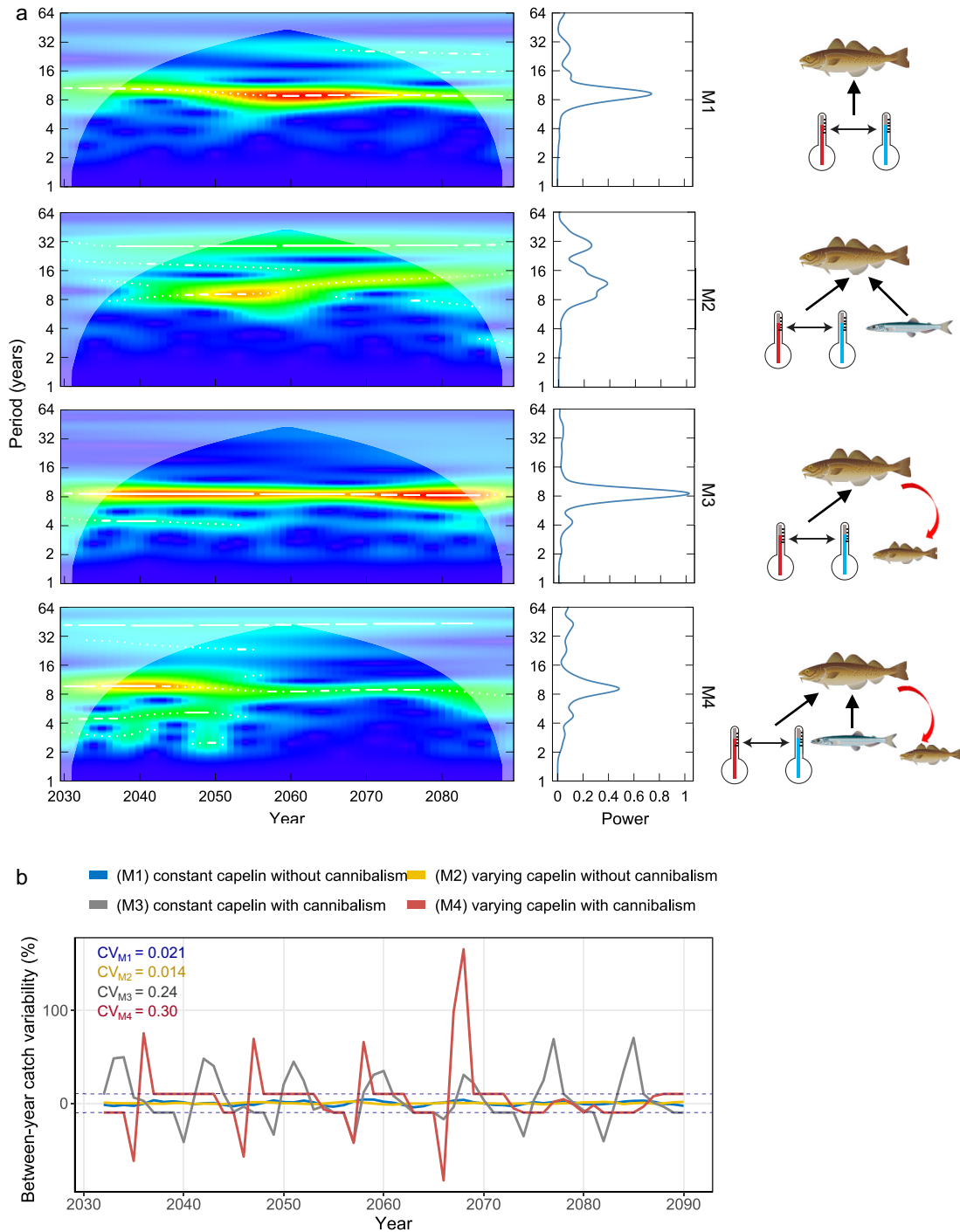


Fig. 2. Ecological uncertainty in Barents Sea cod catch projections using a stochastic, food-web model (StoCoBar under a $\pm 10\%$ constraint). (a) Wavelet power spectra [local (time series, left) and global (time-averaged, right)] of catch projected with different model configurations: constant capelin biomass (1000 t) and varying sea temperature without cannibalism (M1), varying capelin biomass and temperature without cannibalism (M2), constant capelin biomass and varying temperature with cannibalism (M3), and varying capelin biomass and temperature with cannibalism (M4). Red areas of wavelet spectra indicate higher power (intensity of periodicities), blue areas indicate lower power, white areas indicate regions influenced by edge effects (outside the “cone of influence”) in which inferences cannot be made (Cazelles et al. 2014), and y-axis is in the logarithms to the base 2. Spectral plots are based on average wavelet transformations (a wavelet is computed for each simulation individually). (b) Time series (2031–2090) of between-year catch variability (interannual catch variability, ICV, %) computed from simulations (averaged across replicates) with different model configurations (M1–M4). CVs indicate the coefficients of variation computed across years. Horizontal dashed lines indicate a $\pm 10\%$ constraint.

and then destabilized catch as shown in wavelets with weaker, irregular signals (Fig. 2a).

Cod dynamics under yield stability control

Under the baseline scenario with M4, simulated population status and harvest were aligned closely with the historical patterns of Barents Sea cod (ICES 2011; see Appendix S2 for more detailed results) with ICVs (averaged across replicates and years) of 8%. When we constrained ICVs to $\pm 30\%$ or less, mean adult and juvenile biomass, stock size, juvenile survival, and catch all increased; for example, catch was on average as much as 22% higher with a 10% constraint (Fig. 3a). But because juveniles increased at lower rates than adults, juvenile to adult biomass ratios declined by up to 14% with ICVs constrained (Fig. 3a). This trend reflects increasingly intensified density-dependent regulation of recruitment and juvenile survival through cannibalism by more abundant adults competing for food under tight constraints. Wavelet transformation further revealed that the stability control modified the temporal dynamics of not only catch target but also cod population behavior (Fig. 3b; Appendix S2: Figs. S1, S2). When ICVs became increasingly more constrained, the periodicities of stock size and adult biomass remained similar (~ 9 -yr cycles), but the amplitudes gradually increased (Fig. 3b; Appendix S2: Fig. S2a–c). And the dominant periodicity of juvenile survival, which is characterized by a bimodal spectrum, shifted from high frequencies (~ 4 -yr cycles) to low frequencies that eventually match with the periodicity of adult biomass (10-yr cycles, Fig. 3b). This shift reflects the effects of the stability control propagating through life-history processes to dampen the frequencies of strong year classes, forming the divergent trends of juvenile and adult biomass.

Cod stock size and fishing mortality rate fluctuated increasingly out of phase as the stability control became strengthened; oscillations in fishing mortality rate in particular became progressively more amplified (Fig. 4a). Cross-wavelet analyses revealed the unsynchronized signals (with ~ 4 – 5 yr delays) converging to 8-yr dominant cycles (which were shortened from 9-yr cycles) with increasing amplitudes (Fig. 4b; Appendix S3: Fig. S3), indicating greater asynchrony. These emergent, transient patterns stem primarily from delayed density-dependent feedbacks triggered by increasingly more frequent applications of the stability control (33%, 55%, and 70% of the projection years under 30%, 20%, and 10% constraints, respectively). The frequent applications of the stability control temporarily decouple changes in fishing pressure from those in stock size, creating time lags; by constraining ICVs, fishing pressure would rise as long as the SSB exceeds B_{pa} even when stock size starts declining (Fig. 4a). As soon as the SSB falls below B_{pa} , fishing pressure would decline sharply because ICVs are no longer constrained. Also, the stability control would not be reapplied until the SSB rebuilds above B_{pa} , allowing

gradual increases in fishing pressure (Fig. 4a). This harvest measure thus can not only generate asynchronies between the cycles of stock size and fishing pressure but also asymmetries in the cyclicity of fishing pressure.

Stability–sustainability tradeoffs

Although average catches increased (by 10–22%) with the strength of stability control (Fig. 3a), overharvest risks also became increasingly greater owing primarily to high mean ICVs (Fig. 5). When we set ICVs to 30% or higher, the probability of SSBs falling below B_{lim} remained $< 2\%$ (Fig. 5). By contrast, when we constrained ICVs to $< 30\%$, SSBs fell below B_{lim} more often (up to 6.5%) because of greater amplitudes induced by the unsynchronized stock–fishery cycles triggered by strict stability controls (Fig. 4).

DISCUSSION

Our results show that management to suppress short-term yield fluctuations without accounting for the interplay between intrinsic and extrinsic dynamics can inadvertently intensify fishing pressure, amplify long-term yield fluctuations, and destabilize stock–fishery dynamics, thereby posing greater overharvest risk. These patterns are contrasted with the latest evaluation of the cod harvest rules that assume constant environments, showing declined catch variability (ICES 2016). The undesirable and counterintuitive outcomes of yield stability control arise because suppressing variability in catch targets can force fishing pressure to become out of sync with changes in stock abundance. Although stricter controls (30% or less) theoretically give higher average yields because of frequent surges in stock abundance resulted from overcompensation, asynchronies in the stock–fishery dynamics would jeopardize the sustainability of the fishery. This case study with Barents Sea cod further reveals that the stability control, by generating unstable transient stock–fishery dynamics, also can intensify density-dependent regulation of juvenile survival through cannibalism and shift recruitment cycles when prey density and sea temperature stochastically vary. Applying and evaluating management measures with incorrect ecological assumptions of a harvested predator–prey complex thus may overestimate population resilience, thereby underestimating depletion risk and delaying management action.

Fishing-induced cascades of density dependence

Magnified variability in population abundance and yield, a key finding from our study, is also widely reported for size (and age)-selective harvesting (Hsieh et al. 2006). But the underlying mechanisms differ; yield stability control alters the demographics of harvested populations by inadvertently exciting fishing pressure and then intensifying density-dependent regulation, not

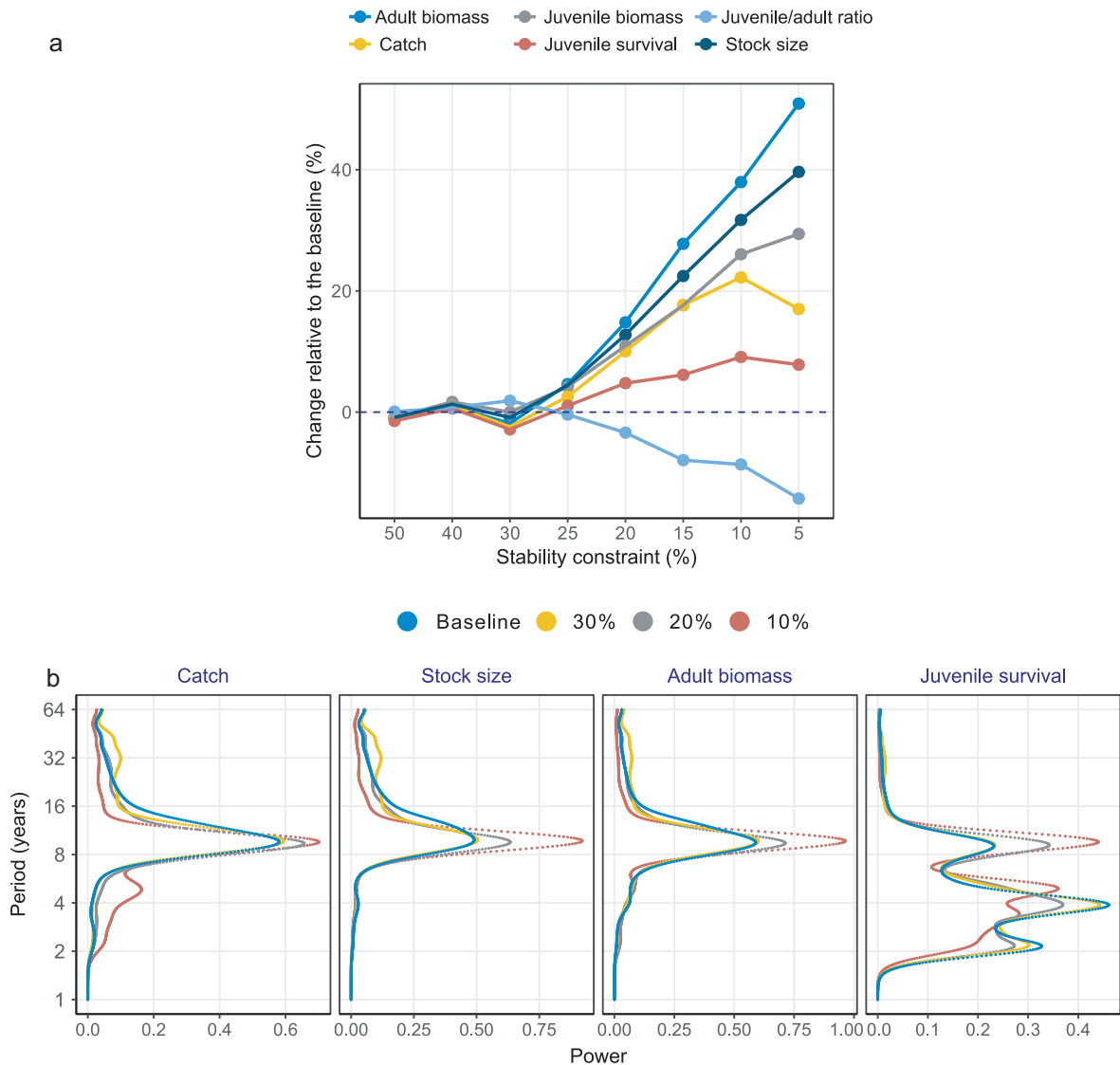


FIG. 3. Fluctuations in Barents Sea cod population behavior and catch projected with a stochastic, food-web model (StoCoBar configuration M4) under varying levels of yield stability control. (a) Proportional changes in catch, harvestable (three-year-olds and older) biomass (stock size), adult biomass (SSB), juvenile biomass, juvenile to adult biomass ratio, and juvenile survival (abundance of three-year-olds) under varying constraints ($\pm 50\%$, $\pm 40\%$, $\pm 30\%$, $\pm 25\%$, $\pm 20\%$, $\pm 15\%$, $\pm 10\%$, and $\pm 5\%$) relative to the baseline simulations. The relative changes are computed based on population metrics averaged across years and replicates. (b) Time-averaged (global) wavelet power spectra of catch, harvestable (three-year-olds and older) biomass (stock size), adult biomass (SSB), and juvenile survival (abundance of three-year-olds) under baseline, $\pm 30\%$, $\pm 20\%$, and $\pm 10\%$ constraints. Y-axis is in the logarithms to the base 2. Spectral plots are based on average wavelet transformations (a wavelet is computed for each simulation individually).

by systematically truncating age structure (Anderson et al. 2008). Suppressing short-term yield variability can impede management responses (time lags in adjusting fishing pressure) to fluctuating stock abundance, in which fishing pressure becomes progressively out of sync with stock abundance, as shown by our analysis. In effect, the stability control can act as quasiperiodic pulse perturbations interacting with stochastic environments, generating transient quasicycles in fishing pressure that sustain for several generations in long-lived species with slow growth like Barents Sea cod. As a result,

harvested populations may display eruptive behaviors in response to pronounced variability in fishing pressure, which then prompts even more applications of the yield-stabilizing measure. These adverse effects are likely to be further exacerbated in lagged management cycles (Kell 2005b).

The transient population cycles also can trigger cascading density-dependent nonlinear feedbacks in cannibalistic predators like Atlantic cod. Yield stability control magnifies variability not only in adult survival rates but also indirectly in reproduction and juvenile survival rates

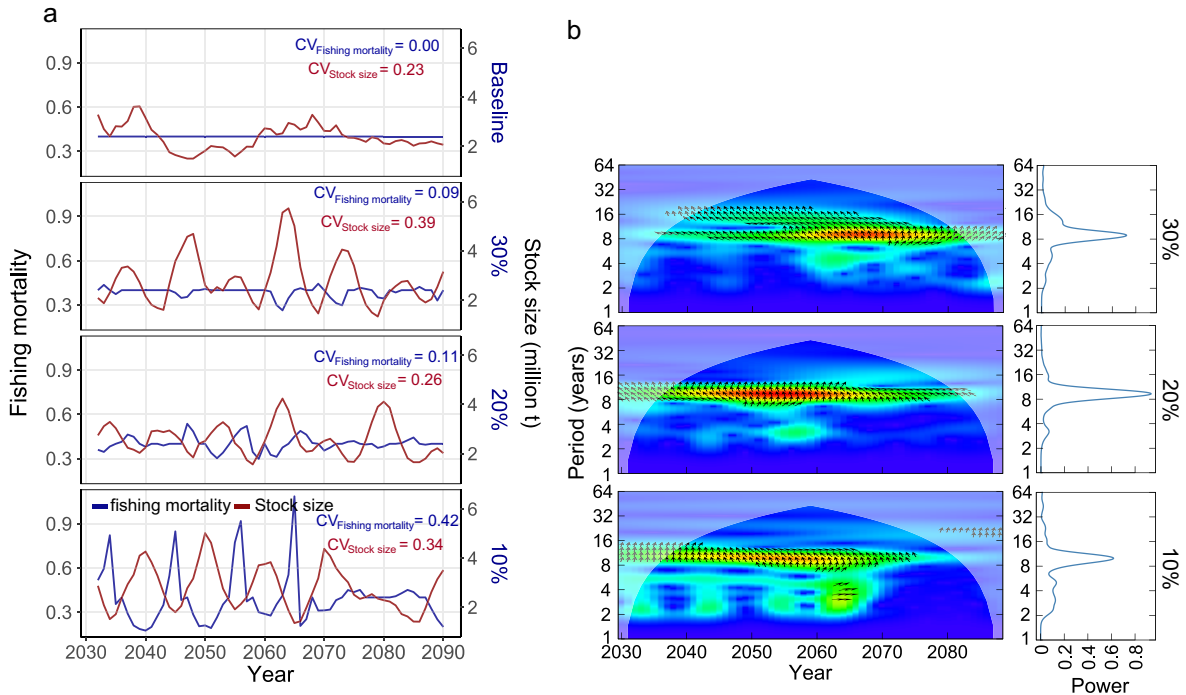


FIG. 4. Synchrony of Barents Sea cod stock abundance and fishing pressure projected with a stochastic, food-web model (StoCoBar configuration M4) under varying levels of yield stability control. (a) Time series (2031–2090) of harvestable (three-year-olds and older) biomass (stock size) and fishing mortality rate (averaged across replicates) under baseline, $\pm 30\%$, $\pm 20\%$, and $\pm 10\%$ constraints. (b) Cross-wavelet power spectra [local (times series, left) and global (time-averaged, right)] between cod stock size and fishing mortality rate under $\pm 30\%$, $\pm 20\%$, and $\pm 10\%$ constraints. Red areas indicate higher power (intensity of periodicities), blue areas indicate lower power, white areas indicate regions influenced by edge effects (outside the “cone of influence”) in which inferences cannot be made (Cazelles et al. 2014), and y-axis is in the logarithms to the base 2. Arrows indicate the two series being in-phase (pointing right), the two series being anti-phase (left), stock size being leading (down), and fishing mortality rate being leading (up). Spectral plots are based on average cross-wavelet transformations (a wavelet is computed for each simulation individually).

by attenuating and intensifying the strength of density dependence in intra- and intercohort interactions, as illustrated by our Barents Sea cod case. Analyses show that the periodicities of stock and catch fluctuations converge toward frequencies that reflect cod life histories, the dominant ages of reproductive adults (six- to nine-year-olds; Appendix S2: Fig. S2) filtering extrinsic signals, a phenomenon called cohort resonance predicted by theory (Bjørnstad et al. 2004, Worden et al. 2010) and demonstrated empirically (Rouyer et al. 2012, Botsford et al. 2014). Under strong stability controls the amplitudes of these dominant frequencies are magnified by more variable fishing pressure, both intensifying and attenuating the strength of density-dependent regulation of juvenile cod survival through the interplay of cannibalism and predation on capelin by adult cod. This finding of enhanced delayed density dependence mediated by trophic interactions supports statistical evidence of capelin’s greater role in cod dynamics under harvesting (Durant et al. 2008). Our simulations further indicate that, following years of high fishing pressures, more juveniles are released from cannibalism, survive, mature, and contribute to adult biomass rebuilding, promoting a surge in stock abundance later (overcompensation through sequential density dependence, Claessen et al. 2004). But

greater adult abundances also intensify cannibalistic pressure on juveniles and ultimately cause shifts in early life histories producing strong year classes less frequently, which would explain a reduction in average juvenile to adult ratios under simulated strong stability controls.

Managing for stability and sustainability

Our study also stresses the timescales of variability; management that suppresses short-term variability in ecosystem services such as harvestable biomass can magnify long-term yield variability and overharvest risk under stochastic environments. The findings suggest an attempt to reduce variability in a managed resource may not reduce its variation but shift its periodicity instead, as predicted by theory (Carpenter et al. 2015) and also shown for other Northeast Atlantic predators (Kell et al. 2005a, 2006). Analyses by Kell et al. (2005a) indicate that the amplification of long-term variability in stock abundance and yield may emerge from time lags in management to detect and respond to changes in harvested populations. Our case study with Barents Sea cod further reveals that the redistribution of period-dependent variability (from short to long term) is modified by time-varying, stage-specific interactions of intrinsic deterministic and

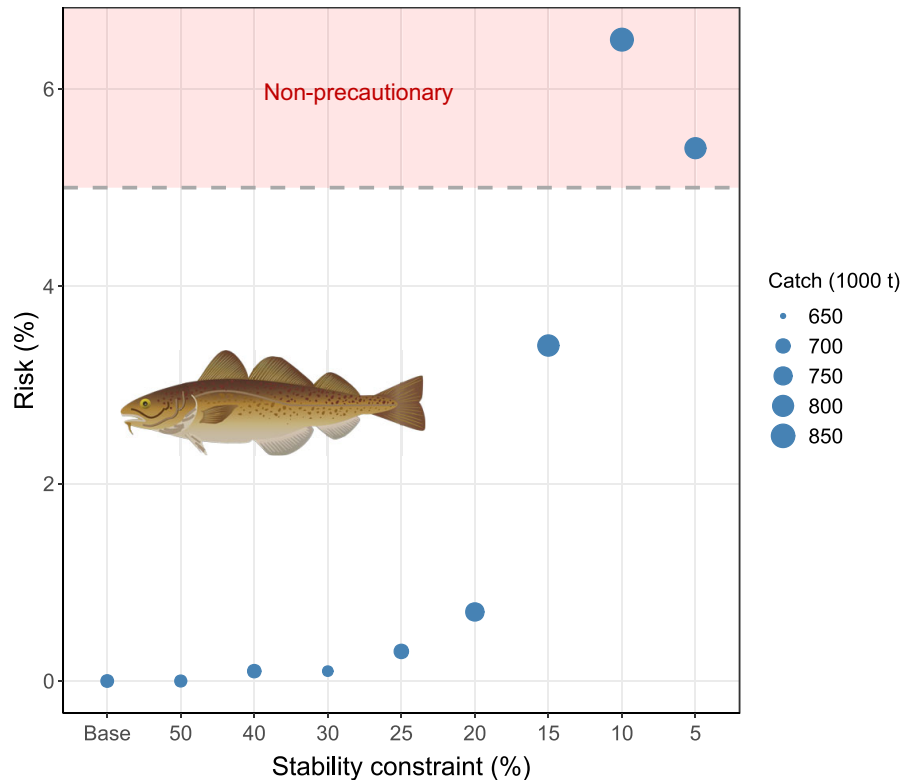


FIG. 5. Catch and overharvest risk of Barents Sea cod projected with a stochastic, food-web model (StoCoBar configuration M4) under varying levels of yield stability control. Risk is based on the probability of adult biomass (SSB) falling below the biological limit threshold ($B_{lim} = 220,000$ t, ICES 2016). The gray horizontal dashed line indicates the risk criterion for reproductive capacity of the population becoming impaired (5%). The red area indicates risk levels considered unacceptable (non-precautionary) by fishery managers.

extrinsic stochastic processes incited by yield stability controls, non-linearly amplifying variations in demographics and stock abundance. Although the stability control for Barents Sea cod has been recently relaxed (from 10% to 20%; ICES 2016), analyses also suggest that even moderate levels of constraints ($\geq 30\%$) still can destabilize cod dynamics when accounting for environmental (often auto-correlated or “red-shifted”) fluctuations in the sea, thereby increasing the probabilities of crossing overharvest and collapse thresholds (reshaping “safe operating space;” Carpenter et al. 2015, Nyström et al. 2019). Management to stabilize fishery yield thus may erode the resilience of a harvested population, making it more sensitive to environmental fluctuations.

Although big variations in fishery yields are disfavored by harvesters and seafood processors, natural variability of a harvested population may give us valuable information about its status such as resilience to changing extrinsic pressures (Carpenter et al. 2015, Nyström et al. 2019). Cyclic behavior with progressively magnified amplitudes for example may warn us about impending collapses of managed resources like salmon populations (White et al. 2014). In effect, by suppressing short-term yield variability we could be trading greater long-term uncertainty for short-term predictability.

Rather than approaches that impose apparent stability, stability in exploited natural resources may be more effectively achieved with promoting resilience and resistance through alternative policy tools that can account for social–ecological dynamics (Carpenter et al. 2015) like marine reserves (Kritzer 2004) and catch shares (Essington 2010). A few large, well designed marine reserves can promote temporal stability in catch by protecting the population structure of harvested species (Nowlis and Roberts 1999, Babcock et al. 2010), thereby buffering noncompliance by commercial harvesters (Kritzer 2004), which can pose excessive fishing pressure and in turn amplify catch variation. By contrast, catch shares can reduce uncertainty in management policy implementation by promoting compliance by harvesters (by ending “the race-to-fish”) and thus improving the performance of management strategies designed to prevent overfishing (Essington 2010).

Model uncertainties

Our model makes several implicit and explicit assumptions that warrant some discussion. First, the model accounts for only indirect effects of prey density (competition, cannibalism, etc.). But direct food-dependent

mortality (starvation) also may contribute to nontrivial variation in survival rates especially in early life (Leggett and DeBlois 1994). Neglecting this uncertainty may have underestimated year-to-year stock and yield variations. Second, the model accounts for cannibalism only as a source of predation mortality in juvenile cod; by excluding predation by other predators we may have overestimated the contribution of cannibalism to the variability in juvenile cod survival rates in some years. Third, we assume no error in assessment on current and recent past status of the stock and implementation of management measures. Historical records also tell us that the scientific advice on yield stability has not always been followed by managers; realized catch targets and landings in the Northeast Atlantic for example generally varied less than recommended (Patterson and Résimont 2007). Our estimates of overharvest risk for alternative harvest measures thus are likely to be conservative. Last, the model inherently assumes structural uncertainty remains unchanged under variable environments. For example, the Ricker relationship for cod reproduction (adult biomass, recruit number, and sea temperature) informed by the historical data may not hold as environmental (climate) variables change (Myers 1998), thereby having unknown consequences of applying management measures when making catch forecasts. The model also assumes that our knowledge about the system does not change over time: no feedback through observation and learning from monitoring and assessment. Future research would benefit from evaluating the robustness of policies by accounting for various sources of uncertainty under a range of environmental variables through simulations of resource–management feedbacks (management strategy evaluation, Punt et al. 2016).

Strategies of managing connected resources

A myriad of ecosystem processes regulating survival of harvested predators interactively influence how given management strategies perform in practice. Applying control measures without accounting for uncertainty in these processes can have unintended consequences (Botsford and Castilla 1997). Our case study with the Atlantic cod–capelin system illustrates that management to suppress yield fluctuations can bring about counterintuitive, adverse outcomes and have far-reaching consequences for living marine resources when failing to account for stochastically fluctuating environments. This amplitude-suppressing policy can generate unstable, high-amplitude cycles akin to those of short-lived species by intensifying density dependence in early life. Given the prominent role cod plays in North Atlantic ecosystems, changes in cod fluctuations may reverberate throughout the rest of the food webs with various consequences for other managed resources and unmanaged resources (Lilly et al. 2008, Frank et al. 2011). In many cod-dominated systems, relatively species-poor systems like the Barents and Baltic Seas and Greenland waters,

in particular, changes in productivity probably propagate further and may amplify or attenuate fluctuations in early life events and population sizes of exploited predators (Lilly et al. 2008, Frank et al. 2011). For example, declined adult cod survival by overharvest may release smaller bodied mesopredators like herring from predation, promoting resource competition with and predation on young cod (Lilly et al. 2008). Because abundant forage fishes like capelin also support other predators as food in the North Atlantic, their declines also may trigger a series of trophically mediated processes including increased consumption of juvenile cod by marine mammals like harp seals in the Barents (Bogstad et al. 2015) and elsewhere (Lilly et al. 2008).

Our findings also highlight broader implications of ecological uncertainty when designing and analyzing management policies for ecologically connected populations. Applying policies without accounting for the dynamic interplay of extrinsic (human exploitation and environment) and intrinsic (life history and demography) fluctuations may fundamentally reshape population structure and behavior of harvested animals, thereby underestimating or overestimating risks of population decline and possibly collapse (Carpenter et al. 2015). With projected changes (both mean and variance) in climate variables and ocean productivity in the coming decades (Wassmann et al. 2011), approaches tailored to specific social–ecological contexts, as demonstrated here, would help develop robust policies that safeguard against such risks and sustainably manage living marine resources while securing socioeconomic stability.

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LITERATURE CITED

- Anderson, C. N., C.-H. Hsieh, S. A. Sandin, R. Hewitt, A. Hallowell, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452:835.
- Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. Lafferty, T. R. Mcclanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences of the United States of America* 107:18256–18261.
- Barraquand, F., et al. 2017. Moving forward in circles: challenges and opportunities in modelling population cycles. *Ecology Letters* 20:1074–1092.
- Bjornstad, O. N., R. M. Nisbet, and J. M. Fromentin. 2004. Trends and cohort resonant effects in age-structured populations. *Journal of Animal Ecology* 73:1157–1167.

- Bogstad, B., G. E. Dingsør, R. B. Ingvaldsen, and H. Gjøsæter. 2013. Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea. *Marine Biology Research* 9:895–907.
- Bogstad, B., H. Gjøsæter, T. Haug, and U. Lindstrøm. 2015. A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Frontiers in Ecology and Evolution* 3:29.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277:509–515.
- Botsford, L. W., M. D. Holland, J. C. Field, and A. Hastings. 2014. Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of Marine Science* 71:2158–2170.
- Carpenter, S. R., W. A. Brock, C. Folke, E. H. Van Nes, and M. Scheffer. 2015. Allowing variance may enlarge the safe operating space for exploited ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 112:14384–14389.
- Carscadden, J., K. Frank, and W. Leggett. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. *Canadian Journal of Fisheries and Aquatic Sciences* 58:73–85.
- Cazelles, B., K. Cazelles, and M. Chavez. 2014. Wavelet analysis in ecology and epidemiology: impact of statistical tests. *Journal of the Royal Society Interface* 11:20130585. <https://royalsocietypublishing.org/doi/10.1098/rsif.2013.0585>
- Cazelles, B., M. Chavez, D. Berteaux, F. Ménard, J. O. Vik, S. Jenouvrier, and N. C. Stenseth. 2008. Wavelet analysis of ecological time series. *Oecologia* 156:287–304.
- Claessen, D., A. M. De Roos, and L. Persson. 2004. Population dynamic theory of size-dependent cannibalism. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271:333–340.
- Cury, P. M., Y. J. Shin, B. Planque, J. M. Durant, J. M. Fromentin, S. Kramer-Schadt, N. C. Stenseth, M. Travers, and V. Grimm. 2008. Ecosystem oceanography for global change in fisheries. *Trends in Ecology & Evolution* 23:338–346.
- Cushing, D. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Pages 249–293 in J. H. S. Blaxter, and A. J. Southward, editors. *Advances in marine biology*. Academic Press, London, UK. <https://www.sciencedirect.com/science/article/pii/S0065288108602023>
- Dingsør, G. E., L. Ciannelli, K.-S. Chan, G. Ottersen, and N. C. Stenseth. 2007. Density dependence and density independence during the early life stages of four marine fish stocks. *Ecology* 88:625–634.
- Dolgov, A. 2002. The role of capelin (*Mallotus villosus*) in the foodweb of the Barents Sea. *ICES Journal of Marine Science* 59:1034–1045.
- Durant, J. M., D. Ø. Hjermann, P. S. Sabarros, and N. C. Stenseth. 2008. Northeast arctic cod population persistence in the Lofoten-Barents Sea system under fishing. *Ecological Applications* 18:662–669.
- Essington, T. E. 2010. Ecological indicators display reduced variation in North American catch share fisheries. *Proceedings of the National Academy of Sciences of the United States of America* 107:754–759.
- Essington, T. E., J. N. Sanchirico, and M. L. Baskett. 2018. Economic value of ecological information in ecosystem-based natural resource management depends on exploitation history. *Proceedings of the National Academy of Sciences of the United States of America* 115:1658–1663.
- Frank, K. T., B. Petrie, J. A. Fisher, and W. C. Leggett. 2011. Transient dynamics of an altered large marine ecosystem. *Nature* 477:86.
- Frank, K. T., B. Petrie, W. C. Leggett, and D. G. Boyce. 2016. Large scale, synchronous variability of marine fish populations driven by commercial exploitation. *Proceedings of the National Academy of Sciences of the United States of America* 113:8248–8253.
- Garcia, S. M., and A. A. Rosenberg. 2010. Food security and marine capture fisheries: characteristics, trends, drivers and future perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2869–2880.
- Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia* 83:453–496.
- Gjøsæter, H., B. Bogstad, and S. Tjelmeland. 2009. Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Marine Biology Research* 5:40–53.
- Gjøsæter, H., S. Tjelmeland, and B. Bogstad. 2012. Ecosystem-based management of fish species in the Barents Sea. Pages 333–352 in G. H. Kruse, H. I. Browman, K. L. Cochrane, D. Evans, G. S. Jamieson, P. A. Livingston, D. Woodby, and C. I. Zhang, editors. *Global progress in ecosystem-based fisheries management*. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks, Alaska, USA. <https://doi.org/10.4027/gpebfm.2012>
- Halley, J. M., and K. I. Stergiou. 2005. The implications of increasing variability of fish landings. *Fish and Fisheries* 6:266–276.
- Hilborn, R., and C. J. Walters. 2013. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Springer Science & Business Media, Boston, Massachusetts, USA. <https://doi.org/10.1007/978-1-4615-3598-0>
- Howell, D., A. A. Filin, B. Bogstad, and J. E. Stiansen. 2013. Unquantifiable uncertainty in projecting stock response to climate change: example from North East Arctic cod. *Marine Biology Research* 9:920–931.
- Hsieh, C.-H., S. M. Glaser, A. J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature* 435:336–340.
- Hsieh, C.-H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. *Nature* 443: 859–862.
- ICES. 2011. Report of the Arctic Fisheries Working Group (AFWG), 28 April - 4 May 2011. Hamburg, Germany. ICES CM 2011/ACOM:05. Pages 659. <https://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2011/AFWG/AFWG%20Report%202011.pdf>
- ICES. 2016. Report of the Second Workshop on Management Plan Evaluation on Northeast Arctic Cod and Haddock and Barents Sea Capelin (WKNEAMP-2), 25–28 January 2016, Kirkenes, Norway. ICES CM 2016/ACOM:47. Page 104.
- ICES. 2019a. Arctic Fisheries Working Group (AFWG). ICES Scientific Reports. 1:30. Paeg 934. <https://doi.org/10.17895/ices.pub.5292>
- ICES. 2019b. Workshop on guidelines for management strategy evaluations (WKG MSE2). ICES Scientific Reports. 1:33. Pages 162.
- ICES 2019c. Workshop on north sea stocks management strategy evaluation (WKNSMSE). ICES Scientific Reports. 1:12. Page 378.
- Ingvaldsen, R., H. Loeng, G. Ottersen, and B. Ådlandsvik. 2003. Climate variability in the Barents Sea during the 20th century with focus on the 1990s. *ICES Marine Science Symposium* 219:160–168.
- Jones, B. 1978. The potential contribution of cod from Greenland to the fishery at Iceland. Technical report. ICES CM 1978/G: 17:15.

- Kell, L., M. Pastoors, R. Scott, M. Smith, F. Van Beek, C. O'Brien, and G. Pilling. 2005a. Evaluation of multiple management objectives for Northeast Atlantic flatfish stocks: sustainability vs. stability of yield. *ICES Journal of Marine Science* 62:1104–1117.
- Kell, L. T., et al. 2005b. An evaluation of the implicit management procedure used for some ICES roundfish stocks. *ICES Journal of Marine Science* 62:750–759.
- Kell, L. T., et al. 2006. An evaluation of multi-annual management strategies for ICES roundfish stocks. *ICES Journal of Marine Science* 63:12–24.
- Kjesbu, O. S., B. Bogstad, J. A. Devine, H. Gjøsæter, D. Howell, R. B. Ingvaldsen, R. D. Nash, and J. E. Skjæraasen. 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences of the United States of America* 111:3478–3483.
- Kritzer, J. P. 2004. Effects of noncompliance on the success of alternative designs of marine protected-area networks for conservation and fisheries management. *Conservation Biology* 18:1021–1031.
- Leggett, W., and E. Deblois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* 32:119–134.
- Lilly, G. R., K. Wieland, B. J. Rothschild, S. Sundby, K. Drinkwater, K. Brander, G. Ottersen, J. E. Carscadden, G. B. Stenson, and G. A. Chouinard. 2008. Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic. Pages 39–66 in G. H. Kruse, K. F. Drinkwater, J. N. Ianelli, J. S. Link, D. L. Stram, V. Wespestad, and D. Woodby, editors. *Resiliency of gadic stocks to fishing and climate change*. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks, Alaska, USA. <https://doi.org/10.4027/rgsfcc.2008>
- Lindgren, M., D. M. Checkley, T. Rouyer, A. D. MacCall, and N. C. Stenseth. 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proceedings of the National Academy of Sciences of the United States of America* 110:13672–13677.
- Link, J. S., B. Bogstad, H. Sparholt, and G. R. Lilly. 2009. Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries* 10:58–87.
- Minto, C., R. A. Myers, and W. Blanchard. 2008. Survival variability and population density in fish populations. *Nature* 452:344.
- Myers, R. A. 1998. When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries* 8:285–305.
- Nowlis, J. S., and C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin* 97:604–616.
- Nyström, M., J.-B. Jouffray, A. V. Norström, B. Crona, P. S. Jørgensen, S. Carpenter, Ö. Bodin, V. Galaz, and C. Folke. 2019. Anatomy and resilience of the global production ecosystem. *Nature* 575:98–108.
- Øiestad, V. 1994. Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. Pages 17–30 in J. Jakobsson, O. S. Astthorsson, R. J. H. Beverton, B. Björnsson, N. Daan, K. T. Frank, J. Meincke, B. Rothschild, S. Sundby, and S. Tilseth, editors. *ICES Marine Science Symposia*. International Council for the Exploration of the Sea, Copenhagen, Denmark. 1991.
- Patterson, K., and M. Résimont. 2007. Change and stability in landings: the responses of fisheries to scientific advice and TACs. *ICES Journal of Marine Science* 64:714–717.
- Punt, A. E., D. S. Butterworth, C. L. de Moor, J. A. A. De Oliveira, and M. Haddon. 2016. Management strategy evaluation: best practices. *Fish and Fisheries* 17:303–334.
- R Development Core Team. 2019. R: A language and environment for statistical computing [Computer software and manual]. R Foundation for Statistical Computing. www.r-project.org
- Roel, B. A., C. M. O'Brien, and M. J. I. J. O. M. S. Basson. 2004. Management Options for the Blackwater Herring, a Local spring-spawning Stock in the Thames Estuary. *ICES Journal of Marine Science* 61:297–307.
- Roesch, A., and H. Schmidbauer. 2018. WaveletComp: computational wavelet analysis. R package version 1.1. <http://CRAN.R-project.org/package=WaveletComp>
- Rouyer, T., A. Sadykov, J. Ohlberger, and N. C. Stenseth. 2012. Does increasing mortality change the response of fish populations to environmental fluctuations? *Ecology Letters* 15:658–665.
- Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences of the United States of America* 108:7075–7080.
- Sundby, S., and O. Nakken. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science* 65:953–962.
- Vert-pre, K. A., R. O. Amoroso, O. P. Jensen, and R. Hilborn. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences of the United States of America* 110:1779–1784.
- Walters, C. J. 1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. *Journal of the Fisheries Board of Canada* 32:1777–1784.
- Wassmann, P., C. M. Duarte, S. Agusti, and M. K. Sejr. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology* 17:1235–1249.
- White, J. W., L. W. Botsford, A. Hastings, and M. D. Holland. 2014. Stochastic models reveal conditions for cyclic dominance in sockeye salmon populations. *Ecological Monographs* 84:69–90.
- Worden, L., L. W. Botsford, A. Hastings, and M. D. Holland. 2010. Frequency responses of age-structured populations: Pacific salmon as an example. *Theoretical Population Biology* 78:239–249.
- Yaragina, N. A., Y. Kovalev, and A. Chetyrkin. 2018. Extrapolating predation mortalities back in time: an example from North-east Arctic cod cannibalism. *Marine Biology Research* 14:203–216.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2498/full>

OPEN RESEARCH

Data sets utilized for this research are published and publicly available (ICES 2011).