Synergies between climate and management for Atlantic cod fisheries at high latitudes

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The widespread depletion of commercially exploited marine living resources is often seen as a general failure of management and results in criticism of contemporary management procedures. When populations show dramatic and positive changes in population size, this invariably leads to questions about whether favorable climatic conditions or good management (or both) were responsible. The Barents Sea cod (*Gadus morhua*) stock has recently increased markedly and the spawning stock biomass is now at an unprecedented high. We identify the crucial social and environmental factors that made this unique growth possible. The relationship between vital rates of Barents Sea cod stock productivity (recruitment, growth, and mortality) and environment is investigated, followed by simulations of population size under different management scenarios. We show that the recent sustained reduction in fishing mortality, facilitated by the implementation of a "harvest control rule," was essential to the increase in population size. Simulations show that a drastic reduction in fishing mortality has resulted in a doubling of the total population biomass compared with that expected under the former management regime. However, management alone was not solely responsible. We document that prevailing climate, operating through several mechanistic links, positively reinforced management actions. Heightened temperature resulted in an increase in the extent of the suitable feeding area for Barents Sea cod, likely offering a release from density-dependent effects (for example, food competition and cannibalism) through prolonged overlap with prey and improved adult stock productivity. Management and climate may thus interact to give a positive outlook for exploited high-latitude marine resources.

gadoids | population dynamics | quota | ocean warming | polar displacement

Unsustainable harvest of marine fisheries resources is frequently reported as a worldwide problem (1, 2) with important socioeconomic (3, 4) and ecological implications (5). Some question whether proper management is even feasible given the assessment tools available and the common disparity between management advice and landings, where the setting of allowable catch is the result of multiple processes, including political ones (6). Prevailing harvesting regimes have also been challenged (7) and contemporary management procedures of many of the world's leading fisheries nations indirectly criticized (8). Assessment tools are unfortunately limited in the amount of complexity (or biological realism) that can be included, even though it is known that stock dynamics result from the interplay of multiple factors acting on the population, each of which can cause fundamentally different responses (9–12).

Fishing has a strong and direct influence on both total and spawning stock biomass (Fig. S1), through reductions in older fish, spatial contraction of the population, potential loss of subpopulations, alteration of life history traits, and habitat damage (13). Meanwhile, a main effect of climate change is to displace the geographical range of organisms, also including fish (refs. 14–16 and Fig. S1). Climate is also known to directly affect individuals through growth, natural mortality, and food availability and indirectly by affecting spawning times or influencing the choice of spawning grounds (Fig. S1). Other indirect effects may include the advection of key prey items from one area to another (i.e., displacement) or changes to system productivity (17). Because of the different ecological responses, a population may react immediately to a climate signal or, because there are often several physical or biological intermediary steps between the forcing and the ecological trait, have a temporally delayed (lagged) response (11, 18). These complex interactions may cause unexpected disruptions in the ability of a population to withstand or adjust to climate changes, cause populations to become more sensitive to climate variability at interannual to interdecadal scales (9), or cause fishery management schemes to have unexpected results (10). Hence, it is probably impossible to completely disentangle the effects of fisheries and climate on population.

Management plans for fish stocks usually include a number of measures such as regulation of total allowable catch (TAC, a quota) as well as technical regulations and estimations of uncertainty. The criteria used for deciding the TAC is often denoted as a harvest control rule (HCR). Although structurally simple, applications of HCRs are considered advanced management tools (19), especially when containing ecosystem-based elements (20). HCRs aim to regulate fishing effort so that the full stock reproductive potential (SRP) is maintained and the population is kept at the size allowing the highest possible harvest under continued exploitation in the long term (i.e., maximum sustainable yield). Social issues, for example, fishers' involvement, are also important for the success of management plans (21). The first application of HCRs appeared in the 1990s (19).

The commercially valuable Barents Sea (BS) cod (*Gadus morhua*), also referred to as Northeast Arctic cod, population has increased greatly in size in recent years, which has coincided with

Significance

Currently many exploited fish populations, including many of the Atlantic cod stocks, are at historically low levels with widespread concern about whether contemporary management is capable of facilitating population recovery. In contrast, the spawning stock biomass of Barents Sea cod is now at an historic high. Here we demonstrate that successful management actions interacting synergistically with prevailing climate caused this increase. Warming of water masses in the Barents Sea over the last decade positively reinforced management actions. A unique and possibly generic mechanism of climate affecting marine animals at high latitudes, especially when at the polar extreme of their distribution, is identified: adjustment of the suitable feeding area. This adjustment is linked closely to community dynamics and increased stock productivity.

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environmental (e.g., temperature) and fisheries' policy changes. A key management development for the BS cod was the introduction of an HCR in 2004 (22) (further details are given in *SI Materials and Methods*) and a total discard ban. However, this HCR did not come into full effect until illegal, unreported, and unregulated catches were reduced in 2006 and then largely eliminated in 2009. In the following analyses, we used 2007 as the year of implementation because that was the year when fishing mortality (F) was reduced to the level intended in the described management plan. One important consequence of this agreed plan has been that catches have remained within scientific guidelines during the increase in stock biomass.

Could favorable climatic conditions (Fig. 1*A*) alone have resulted in the recent increases in total stock biomass (TSB) and spawning stock biomass (SSB) for BS cod (Fig. 1*B*), or has management also contributed? Have BS managers simply been "lucky" compared with, for instance, managers involved with the Northern cod collapse off Newfoundland (23)? Assuming that the recent warmer regime did not play a role seems unrealistic; temperature is generally positively associated with TSB for BS cod (Fig. 1 *A* and *B*). Climate has the potential to influence cod population dynamics through multiple links (Fig. S1), but disentangling exact mechanisms is difficult. For example, ambient temperature influences biochemical processes for ectotherms (24), but changing fish distributions make the link between regional and ambient temperature difficult to analyze or predict. We therefore assessed the impact of climate and management on BS cod population size in three different ways. First, we investigated how the principal "drivers" of BS cod stock productivity (Fig. 2) related to ocean temperature and spatial distribution, more specifically suitable feeding area extent (SFA), a less common metric in relation to climate effects studies. Second, we modeled what would have happened if the HCR (*i*) had never been implemented and (*ii*) had been implemented in 1993 (i.e., at the beginning of a period of stable growth and mortality). Finally, the consequence of the actual 2007 HCR implementation on fishing patterns was evaluated by studying the development in F for young (3, 4) and older (5–10) age classes.

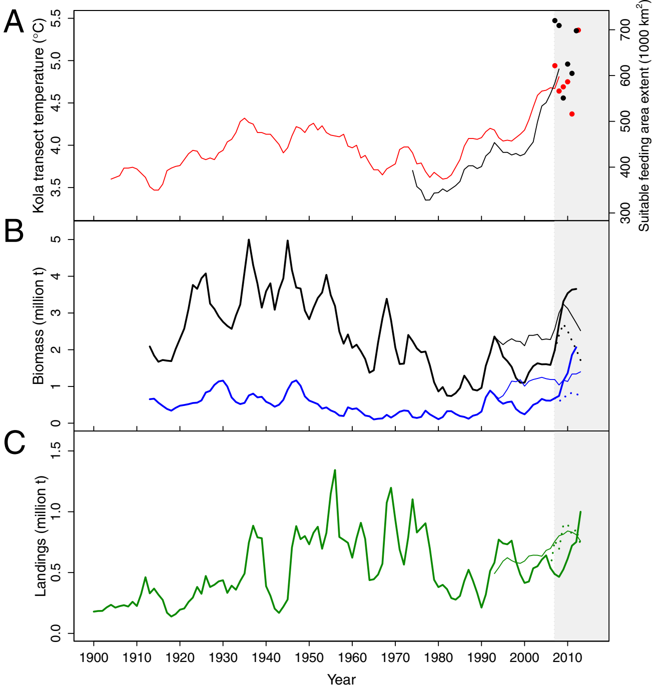

Fig. 1. Both environmental conditions and cod stock metrics have fluctuated greatly in the Barents Sea ecosystem over time. (*A*–*C*) Shaded area indicates the HCR implementation period (2007–2013). (*A*) Nine-year smoothed Kola temperature (red) (1900–2012) and suitable feeding area extent (black) (1970–2012), with real data plotted as points during the HCR implementation period. (*B*) Trends in spawning stock biomass (blue) and total biomass (black) (1913–2012). Actual biomass (solid, thick line) refers to the measured biomass of the population, and simulated HCR (solid, thin line) was estimated as if the HCR had been introduced in 1993. No HCR (dotted line) reflects biomass development under no HCR implementation. (*C*) Landings under the different harvest scenarios (1900–2012).

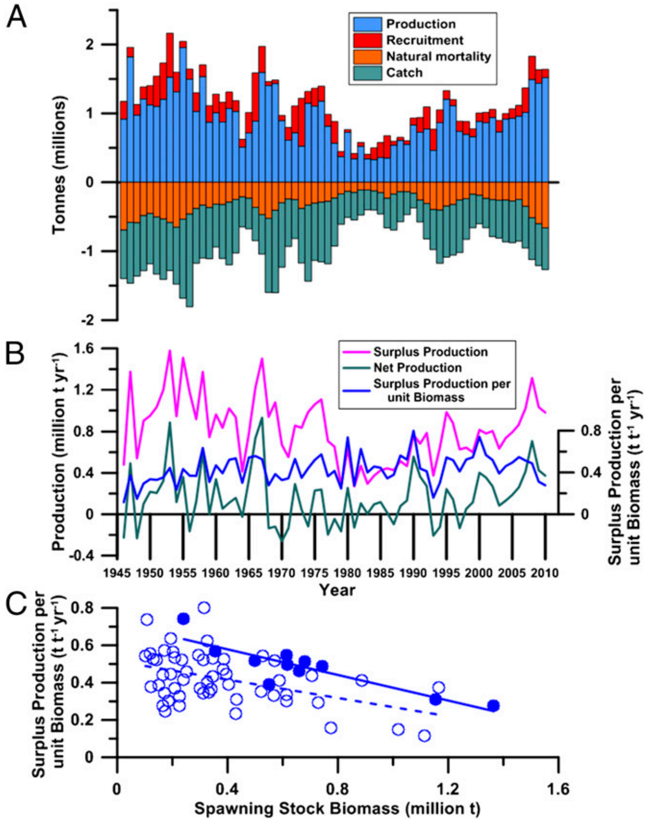

Fig. 2. The BS cod production has peaked several times since WWII but is significantly higher today if standardized per unit biomass. (*A*) Overview of BS cod annual production, recruitment, natural mortality, and catch (1946–2010). (*B*) Corresponding surplus and net production. The difference between surplus production and net production reflects landings. (*C*) Surplus production per unit biomass in relation to spawning stock biomass for the periods 2000–2010 (filled circle and solid line) and 1946–1999 (open circle and dashed line) (ANCOVA, $n = 65$).

Results and Discussion

BS Cod Productivity. The main impact on BS cod productivity was generally expected to be fishing, although the environment was also suspected to have had an impact (25). Surplus production is an indicator of both total stock size and environmental conditions, which either promote or retard individual growth and survival. Productivity of BS cod indicated cyclic patterns in the surplus production (PS_t), partially mirroring trends in stock biomass, with the main peaks appearing in the early 1950s, late 1960s, and in recent years (Figs. 1*B* and 2 *A* and *B*). The trend from 1980 has generally been an increase in PS_t. The effect of the fishery is seen in the net production (PN_t). Net production is an indicator of fishing levels under the prevailing stock productivity regime, where negative values indicate a trajectory toward stock decline and positive values the potential for stock increase. PN_t was positive after the late 1990s but was negative for a number of years in the

1970s through the 1990s (Fig. 2*B*). Overall, PN_t was generally positive, indicating the stock was not severely depleted; fish stocks can only support fisheries in the long term if their reproductive potential and growth (surplus production) is not inhibited by fishing (seen as net production). Enough biomass must be produced to ensure SRP is maintained; otherwise, PS_t will be further curtailed.

In general, in cod stocks, surplus production, especially surplus production per unit biomass, tends to decline when stocks are very large relative to their carrying capacity (25). In line with ref. 25, the surplus production per unit biomass (PS_t/B) has been declining simultaneously with the growth in population since 2000, but not to the low level previously observed when SSB was high (Fig. 2*B*). Using SSB as a covariate, PS_t/B in recent times (2000–2010) was significantly higher than earlier (1946–1999; slope, $P = 0.450$; intercept, $P = 0.001$) (Fig. 2*C*). Hence, the adult BS cod population, during ocean warming (Fig. 1*A*), seems more "productive" than previously. This should, however, be taken as an illustration of the current situation in relation to the historic rather than a regime shift, because the change in conditions has been gradual (Fig. 1 *A* and *B*). BS cod has likely benefited from being at the northern limits of suitable climate for cod, where warming has a positive impact. This is in contrast to more southerly cod stocks (e.g., the North Sea or Georges Bank), where warming may have a neutral or negative effect (26, 27). Historically, the cold-water Northern cod stock was of a similar size to the BS cod (22, 23) but collapsed in the early 1990s owing to overfishing (23). Because of its depleted status, it is difficult to specify the likely effect of climate change on spatial distribution (27). In contrast to BS cod, Northern cod live in an area with a strong latitudinal temperature gradient and a cold southward current (28, 29), which should restrict a northward expansion of the stock. Baltic cod stands out as a special case in which the suitable habitat for early life stages (in terms of sufficient oxygen content and salinity), rather than for the adults, influences the population dynamics in this brackish environment (30, 31).

BS cod is a major consumer of secondary and tertiary production, and therefore BS cod dynamics are closely linked to the abundance of available prey (Fig. S2*A*). The fluctuations in prey abundance, especially for BS capelin (*Mallotus villosus*), are generally reflected in the diet composition of cod, which can be characterized as a generalist feeder with a wide range of suitable prey (Fig. S2*B*). The growth of cod was very slow during the first capelin collapse in the 1980s, a period of relatively low BS cod surplus production. During the second and third collapses in the 1990s and 2000s, cod was able to compensate by switching to other prey so that the growth, and hence surplus production, was little affected by the lack of capelin (Fig. 2).

Temperature Effects on BS Cod Growth and Recruitment. Temperature changes have a considerable effect on the abundance of BS cod through growth and recruitment (R) (32, 33). A significant increase in the amount of warm Atlantic waters inflowing into the BS (34), which also imports food (zooplankton) for juvenile cod (11, 35), has raised temperatures by close to 1.5 °C since the late 1970s (Fig. 1*A*) (36). No convincing evidence indicated a direct temperature influence on survival of early year classes, that is, R/SSB (age 1, $P = 0.06$; age 2, $P = 0.49$; age 3, $P = 0.60$; 1- to 3-y temperature lag, respectively); this is in agreement with earlier studies that showed temperature on its own does not determine year-class strength (37). For the younger ages, higher temperatures were linked to slower growth in length (ages 1 and 2, $P \leq 0.01$; age 3, $P = 0.05$; Table S1) but not weight, and when the effect of stock size (SSB) was included, the temperature effect disappeared ($P > 0.05$). Density-dependent intercohort effects seemed to be stronger for young cod than any direct temperature effect on growth ($P \leq 0.002$; Table S1 and Fig. S3). Length at age of the younger fish was negatively associated with total stock size in the preceding years, whereas such an effect was only found in weight at age of older cod (Fig. S4 and Table S2), as also found by Kovalev and Yaragina (38).

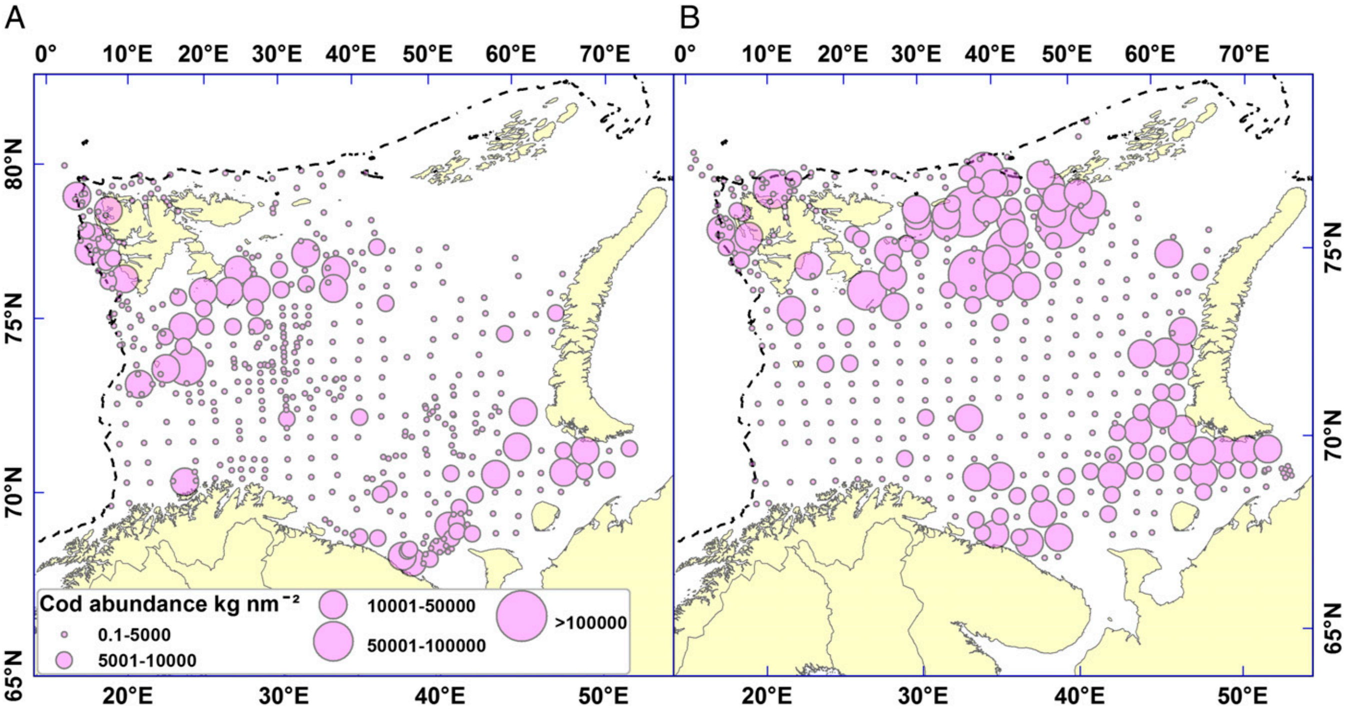

Fig. 3. In recent times, cod have expanded to the northernmost edge of the BS. Distribution of cod catches (kilograms per square nautical mile) from bottom trawls during the (*A*) 2007 and (*B*) 2012 autumn ecosystem surveys. Dashed line indicates 500-m bathymetry contour.

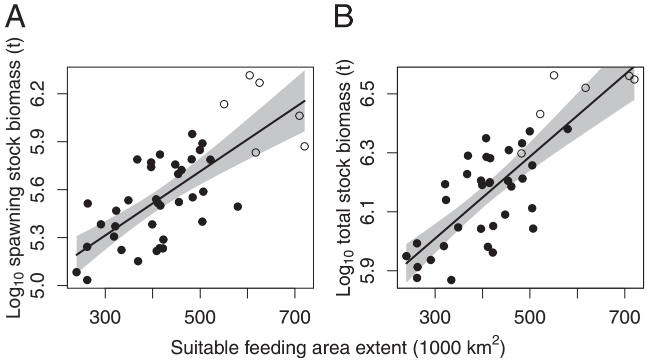

Fig. 4. A larger SFA in the BS supports a higher biomass of cod. Effect of SFA lagged 1 y on (*A*) log$_{10}$-transformed SSB and (*B*) TSB for BS cod (1970–2012). Open circles denote SSB or TSB after implementation of the HCR in 2007.

Temperature-Driven Range Expansions and BS Cod Population Size. Ocean warming contributed positively to the current high biomass of BS cod, predominantly through expansion of the SFA. Increased temperature led to a markedly enlarged SFA for BS cod (immediate effect, $r = 0.81$; one-year lag, $r = 0.62$; $P < 0.001$; Fig. 1*A*). In the late 1970s/early 1980s, $\sim$35% of the BS had conditions suitable for cod, whereas more than 70% of the BS had suitable conditions in the years 2004–2012. With a larger area available for feeding, BS cod are expected to expand their distribution, particularly the adult component (39). This has certainly happened, especially in recent years, when autumn BS cod distributions expanded northward to 80–82°N (Fig. 3). A wider distribution should, in turn, result in increased stock size through greater availability of prey, such as capelin, and recent modeling studies have indicated that greater overlap with capelin has a beneficial impact on cod biomass (40). Furthermore, warming has likely improved capelin productivity by extending their feeding season associated with the ice retreat (41), resulting in higher average biomass and wider distribution since the late 1990s (42). Therefore, the northward expansion of cod gives a greater spatial and temporal overlap with capelin, their principle prey. High BS cod biomass is linked to this substantial expansion, with SFA positively associated with SSB and TSB in the same and following year(s) (Fig. 4, Fig. S5, and Table S3; $P \le 0.003$). Adult fish may have the largest migration potential (43) and respond quickly to changes in the SFA with changes in feeding migration, hence the strong relationship between SFA and SSB at 0- or 1-y lags. However, the relationship between TSB and SFA is stronger at larger lags (e.g., SFA 3 y before). A possible explanation may be that younger fish need several years to expand their feeding grounds or that a larger SFA increases the survival and growth of the younger year classes (44).

In recent years, both the SFA and the stock itself have been large enough to facilitate a widespread cod distribution (Figs. 3 and 4). These results imply greater spatial overlap between BS cod, capelin, and other important prey for longer periods in warmer years (45). No indication of BS capelin or cod distributions expanding into the deep Polar Basin or contraction of distributional ranges northward with warming exists. A purely temporal approach may mask the true underlying relationships that regulate abundance. The integrated effects of this enlarged SFA on the BS cod stock are likely to be substantial.

Role of Management in BS Cod Stock Development. The effects of implementing the HCR (i.e., reducing F) at different times in the simulations of stock development were evaluated at both the stock and harvest levels. An assumed continuation of the previous management regime (no HCR) led to a higher total sum of landings from 2007 to 2013 (Fig. 1*C*), whereas the actual 2007 HCR implementation resulted in significantly higher TSB and SSB (Fig. 1*B*). Annual catches under the HCR did not become greater than those under the previous management regime until 2013. If the HCR had been implemented in 1993, the noticeable decline in TSB and SSB from 1993 through 2000, occurring despite improved temperature conditions, might have been avoided (Fig. 1*B*). The excessively high catches taken in the 1990s and the associated stock decline would not have happened and higher predicted catches from 1999 would have occurred (Fig. 1*C*). Therefore, the initial lowering of catches caused by the HCR is compensated by the long-term gains from higher stock size, although more than one generation of BS cod seems to be needed to obtain a net gain in yield.

An important consequence of the contemporary management regime was the higher survival rate (lower F) of older fish (Fig. 5). Reconstruction of the historic demographic population structure of the stock seems to be occurring (46) (Fig. S6). The truncated age distributions commonly seen in heavily fished populations are known to negatively affect parental quality (47) and thereby recruitment success (48). If this holds true for the BS cod, positive changes in recruitment should become apparent in the near future as a consequence of the higher stock-age diversity (49). Furthermore, having a wider range of reproductive age classes may buffer against factors influencing recruitment variability (e.g., ref. 33). The BS cod population, in which stock size increased with reduced F to the highest recorded level post-WWII, thus provides an excellent opportunity to examine hypotheses on parental effects.

Conclusion

The implementation of a moderate F and a HCR for BS cod, which has been assessed by the International Council for the Exploration of the Sea as sustainable, can be viewed as a management approach effectuating an exploitation rate agreeing with the internationally adopted objective of a precautionary long-term sustainable yield (2). This is an exception, rather than the rule, for commercially important Atlantic cod stocks in recent decades. The lessons learned from BS cod management are clearly transferable to cod in general, other gadoids, and, potentially, other longer-lived teleosts. The current HCR used in BS cod management is expected to be developed further by, for instance,

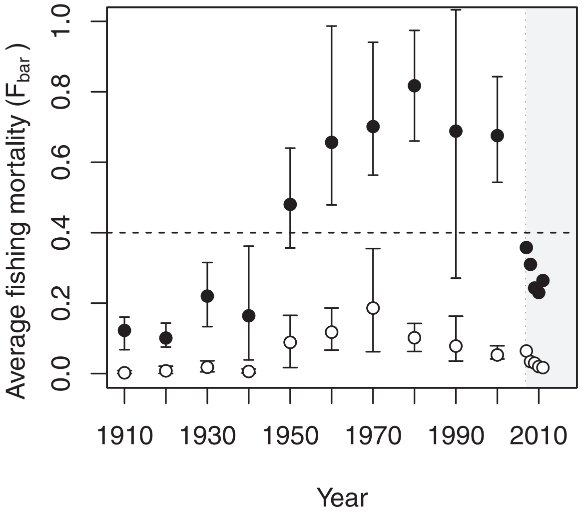

Fig. 5. The low exploitation pattern seen today resembles that of 100 y ago. Average fishing mortality (F$_{\text{bar}}$) for cod ages 3–4 (open circles) and ages 5–10 (filled circles); data are averaged by decade from 1910 until 2006 and then plotted annually up to 2011. Error bars are minimum and maximum values. Shaded region indicates the implementation of the HCR and dotted line refers to precautionary F for ages 5–10.

incorporating environmental variables. The implementation of the new management regime for BS cod was facilitated by the more than 50-y cooperation in science and management between the two key players, Russia and Norway (50). The fact that only two countries/entities were involved simplified the implementation scheme in comparison with, for example, European Union waters (51). Furthermore, the HCR was introduced during a period of moderate stock abundance (Fig. 1*B*). Hence, delayed management effects on rebuilding seriously depleted stocks (13) were not encountered. Despite this, it took more than one generation of BS cod for simulated accumulated catches under the HCR to exceed those predicted without the HCR, indicating the long time scales involved. Ocean warming also contributed positively to the record high biomass through SFA expansion in conjunction with average recruitment and a de facto improved adult PS_t/B. BS cod managers have undoubtedly been fortunate regarding the prevailing climate, but our simulations imply that the adopted management regime was the main success criterion; that it was enacted before the stock had become seriously depleted was also likely critical (13). Hilborn and Litzinger (25), using data up to 2003, state that for most of the Northeast Atlantic cod stocks a reduction in catches would result in substantial stock rebuilding. Using more recent data where F had been reduced, we show an elevated stock size. Arguably, the present population size may be approaching the carrying capacity of the ecosystem (52), although it is difficult to make definitive conclusions in this regard given the ongoing increase in SFA. Previously, when the BS cod stock was very large, the total surplus production and surplus production per unit biomass declined when the stock reached its present level (25). Although the BS cod stock has reached the geographically defined northern limit of its possible range at its maximum extent in late summer, further warming has the potential to allow for expansion to the east and for an overall wider distribution during a larger fraction of the year. Further warming should thus lead to additional increases in SFA. The economic gain from the fishery may be reduced if the market is oversupplied by cod, but the current HCR is believed to maximize economic profits (53). The case of the BS cod shows that if management is underpinned by sound scientific advice and the actors involved both at the national and industry level heed management advice, sustainable exploitation of marine resources is indeed achievable. The use of precautionary biological reference points in applied management has contributed greatly to the highest recorded SSB for the, currently, largest cod stock in the world.

Materials and Methods

Two different metrics were applied to account for the influence of the ecosystem on productivity: recruit per spawner and annual stock productivity. High recruit-per-spawner ratios were assumed to represent high stock production and low ratios, low production. The surplus and net production of the entire stock, including growth of both recruits and nonrecruits, and mortality (natural and fishing) was then estimated using methods similar to those of Dutil and coworkers (e.g., refs. 54 and 55) (*SI Materials and Methods*).

Exceptionally long hydrographic and population time series, supplemented with information on BS cod growth, maturity, consumption, and prey abundance were available. Ocean temperature data came from the Kola Section (70°30′–72°30′N, 33°30′E), which is also a proxy for Atlantic water inflow strength and thereby BS climate conditions (36). The area with bottom water characterized by temperatures appropriate for BS cod [i.e., temperature >0 °C (56)] was used to investigate the influence of annual variation in SFA from 1970 onward (Fig. 1*A*). Stock numbers and weight at age, catch, and natural mortality at age were taken from the international stock assessment on Northeast Arctic (BS) cod (22), whereas the complete BS cod stock time series from 1913 was from ref. 57.

All relationships were investigated with either linear models, analysis of covariance (ANCOVA), generalized least squares (GLS), or generalized additive models. GLS models were used if heteroscedasticity violations occurred when using linear regressions (58). Kola temperature and SSB were standardized to the year of spawning. Standardizing SSB allowed an indirect investigation of the amount of density dependence within a cohort. A large SSB can produce many eggs, leading to a large 0-group year class, which would compete heavily for available resources, the effects of which might persist with age. *SI Materials and Methods* gives a complete description of the data and statistical methods.

Two "what-if" scenarios were constructed: What would have happened if (*i*) the HCR had not been implemented in 2007, and (*ii*) the HCR had been implemented earlier? The former reflects a "status quo" management approach, that is, continuing with a high F on ages 5–10 of 0.62 (the grand mean since 1946 as well as in 2002–2006) instead of 0.40 (the precautionary level) (22). The second scenario modeled biomass development as if the present HCR had been implemented in 1993. This year was chosen because (*i*) the BS temperature was close to the long-term average (Fig. 1*A*), (*ii*) Fs in preceding years (1990–1992) were ∼0.40 (22), (*iii*) growth and maturity were relatively stable after this year (Fig. S2*A*), and (*iv*) recruitment at age 3 approximated the average since 1946 (Fig. 2). The scenarios simulated stock dynamics by varying F in age-structured fisheries dynamics models (*SI Materials and Methods*). The consequence of the HCR implementation on fishing patterns was evaluated by studying arithmetic mean development in F.

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