

Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes

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The relative roles of density dependence and life history evolution in contributing to rapid fisheries-induced trait changes remain debated. In the 1930s, northeast Arctic cod (*Gadus morhua*), currently the world's largest cod stock, experienced a shift from a traditional spawning-ground fishery to an industrial trawl fishery with elevated exploitation in the stock's feeding grounds. Since then, age and length at maturation have declined dramatically, a trend paralleled in other exploited stocks worldwide. These trends can be explained by demographic truncation of the population's age structure, phenotypic plasticity in maturation arising through density-dependent growth, fisheries-induced evolution favoring faster-growing or earlier-maturing fish, or a combination of these processes. Here, we use a multitrait eco-evolutionary model to assess the capacity of these processes to reproduce 74 y of historical data on age and length at maturation in northeast Arctic cod, while mimicking the stock's historical harvesting regime. Our results show that model predictions critically depend on the assumed density dependence of growth: when this is weak, life history evolution might be necessary to prevent stock collapse, whereas when a stronger density dependence estimated from recent data is used, the role of evolution in explaining fisheries-induced trait changes is diminished. Our integrative analysis of density-dependent growth, multitrait evolution, and stock-specific time series data underscores the importance of jointly considering evolutionary and ecological processes, enabling a more comprehensive perspective on empirically observed stock dynamics than previous studies could provide.

phenotypic plasticity | eco-evolutionary dynamics | management | genetic adaptation | genetic variance

Harvesting is usually selective, differentially targeting and removing members of a population based on their phenotypic attributes (1, 2). Such selective harvesting induces a genetic response in life history traits when it renders some genotypes more likely than others to survive and reproduce (3, 4). Even nonselective harvesting can induce evolutionary change, through the effects of elevated mortality on the differential survival and reproduction of individuals with specific genetic attributes (5). During the last decade, progress has been made in identifying evolutionary responses to harvest in the wild (6–8), as improved statistical methods for analyzing field data have become available (9, 10). Although trends in life history traits have repeatedly been found to be indicative of genetic adaptations to intense harvest pressures, their concomitance with phenotypically plastic responses to changing environmental conditions often complicates the identification of genetic changes (3, 4, 11–14). An important type of phenotypic plasticity affects growth rates and maturation schedules and is known as the compensatory response in fisheries science: when increased fishing mortality reduces intraspecific competition, individuals with the same growth genotypes can grow faster and

mature earlier. The difficulty of disentangling such plastic effects and evolutionary changes in empirical data lies at the heart of the debate on fisheries-induced evolution (3, 15–19).

Distinguishing between plastic and genetic responses to harvesting is of considerable practical importance and consequence, because genetic responses (*i*) are often expected to be substantially more difficult and slower to reverse than plastic responses (20–23), (*ii*) alter fundamental processes of population dynamics (24), and (*iii*) could reduce resilience to other stressors such as climate change (25, 26). In addition, there could be economic costs of evolutionary change when fishing mortality is high; alternatively, fisheries-induced evolution can increase profits when fishing mortality is low and a stock's abundance remains above its precautionary level (27). In view of the cumulative and long-term nature of these effects, and in line with a duly precautionary approach to resource management, the potential occurrence of harvest-induced genetic adaptation continues to cause concern (3, 4, 28–30).

Northeast Arctic (NEA) cod (*Gadus morhua*) is one of the world's most important commercial fish stocks and is distributed among feeding grounds in the Barents Sea and spawning grounds

Significance

Rapid anthropogenic trait changes in fish stocks is a highly publicized ocean conservation issue, yet the relative contributions of evolutionary and ecological dynamics are unknown. We present an integrative empirically based simulation model to determine the role of these contributions in the world's largest cod stock. We quantitatively evaluate predictions with different density-dependent growth models using historical stock-specific data. The amount of evolution required for explaining observed maturation trends is small, yet with weakly density-dependent growth, critical for preventing stock collapse. The role of evolution in explaining trends is diminished when density-dependent growth is present. Our study reveals how interactions among evolution, ecology, and fisheries influence stock dynamics and harvest sustainability, emphasizing the need for integrated approaches to fisheries management.

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along the Norwegian coast. Beginning in the 1930s, a substantial increase in fishing intensity and a change in fishing selectivity occurred as trawlers progressively entered the Barents Sea, exposing smaller immature cod to unprecedented levels of exploitation (31). Until then, coastal fishing with conventional gears had dominated the fishery, mainly targeting mature cod in the spawning grounds (32). In the wake of this striking change in exploitation pattern, the mean age at maturation in NEA cod decreased from more than 9 y in the 1930s to 5–6 y in the 2000s (33–35), a decline far greater than what could be explained by changes in aging methodology or changes in assessing maturation (36). One possible explanation of this precipitous decline is a release from density regulation through reduced biomass levels, resulting in improved conditions for somatic growth and enabling earlier maturation through a compensatory response (e.g., refs. 37 and 38). Another, not mutually exclusive, explanation is that the selective pressures imposed by harvesting have elicited an evolutionary response in the population, causing maturation to be initiated earlier in life and at smaller body sizes (28, 35). Similar considerations apply to other fish stocks, including the collapsed northern cod stock off the east coast of Canada (8). Capitalizing on the striking shift in fishing selectivity experienced by NEA cod, and building on a series of systematic long-term data collected since 1932 (Fig. 1 and Fig. S14), here we evaluate the differential contributions and merits of these two explanatory hypotheses.

In addition to a possible genetic response in maturation schedule, harvesting could induce genetic adaptation in numerous other life history traits (22, 29, 39). For example, evolutionary models have predicted that growth rates could evolve to become either faster or slower, depending on the patterns of size selectivity (22,

40, 41). Harvest could also induce genetic changes in reproductive investment if, for example, intense fishing pressure favors individuals that invest more in current reproduction (5, 22, 42).

In this study, we use an empirically based multitrait simulation model that integrates ecological and evolutionary dynamics to examine how density-dependent growth and fisheries-induced evolution contribute to the maturation trends observed in NEA cod. Our model enables evolution of key quantitative traits describing the processes of growth, maturation, and reproductive investment. The model has already been used to study optimal harvesting (43) and the bioeconomic consequences of fisheries-induced evolution (27). Including feedbacks between ecological and evolutionary dynamics is a perspective typically missing in fishery science, despite the implications for management (44). We address this challenge using extensive time series data collected for an important marine fish stock (4). Our main objective and key contribution are to assess the levels of density-dependent growth and fisheries-induced evolution required for achieving good agreement between model predictions and a 74-y time series of age and length at maturation. We extend earlier work in three key directions. First, although eco-evolutionary models have included density-dependent growth (24, 45–48), previous evolutionary models of NEA cod (28, 49–51) did not, and thus could not assess the differential contributions of phenotypic plasticity and trait evolution to the observed maturation trends in this stock. Second, although some eco-evolutionary models have allowed simultaneous evolution of multiple traits (e.g., growth and maturation) (22, 45, 46, 48, 52), most previous studies restricted attention to the evolution of maturation schedules (51, 53–56); here, we consider an evolving maturation schedule in conjunction with the potential for fisheries-induced evolution in two other important life history traits, somatic growth and reproductive investment. Allowing for the simultaneous evolution of these additional traits might reduce the amount of evolution predicted in the maturation schedule, because the processes of growth, maturation, and reproductive investment are naturally intertwined. Third, to our knowledge, previous studies have not statistically compared stock-specific time series data with model predictions, as we do here to evaluate the relative roles of fisheries-induced evolution and density-dependent growth.

To consider the importance of density dependence for the dynamics of NEA cod, we investigate two density-dependent growth models. The first model (the “contemporary growth model”) is estimated for the later part of the time series for which the data allow for a direct estimation of the density dependence of growth (1978–2009), revealing a strong, negative relationship with a high degree of variation explained (*S1. Model Description*). Because this relationship might not be representative of historical conditions, we also estimate a second model (the “historical growth model”) for the beginning of the time series (1932–1950) when the population was larger: the earlier data do not allow for the direct estimation of growth and probably underestimate the strength of its density dependence, but nevertheless suggests a much weaker density dependence of growth, albeit with poorer explanatory power (*S1. Model Description*). The choice of these two time periods provides a good contrast between the two corresponding growth models (i.e., strong versus weak density dependence), enabling us to evaluate the potential role of density-dependent growth using parameters empirically derived for a large marine fish stock.

Our simulation model includes four evolving life history traits: somatic growth capacity, reproductive investment (measured by the gonadosomatic index, GSI), and the intercept and slope of the probabilistic maturation reaction norm (PMRN) characterizing the maturation schedule (10, 12, 34). For both growth models and all evolving traits, we analyze the effects of different coefficients of genetic variation (CV), ranging from 0% to 14% in the initial population. The CV is a measure of the scope for evolution in a given trait (24, 27). When the CVs for all genetic

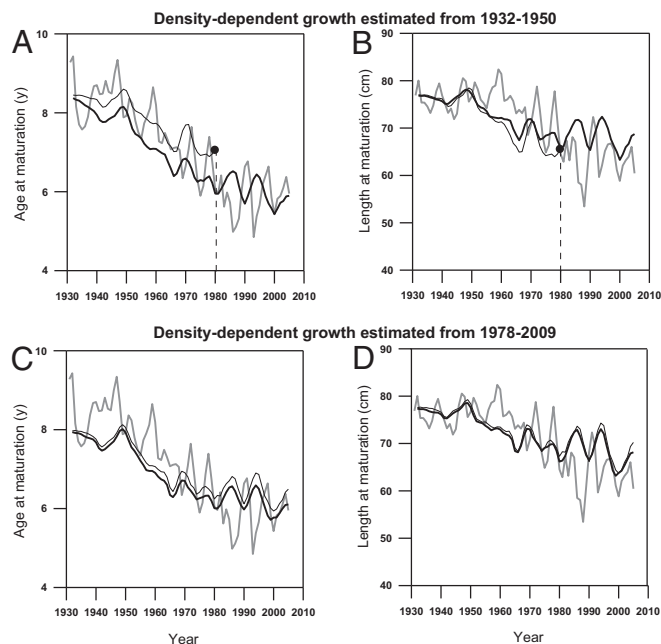


Fig. 1. Comparison of model predictions and observations for age and length at maturation in NEA cod for (A and B) the historical growth model and (C and D) the contemporary growth model. Observations are shown with gray lines; eco-evolutionary model predictions, with thick black lines; and nonevolutionary model predictions, with thin black lines. The shown models possess the highest likelihoods among all 16 model variants and associated CV combinations (Table 1 and *S3. Model Selection*). In A and B, the nonevolving population goes extinct at the point indicated by the filled circles and dashed lines. Model predictions are the mean ages and lengths at maturation among individuals in the population, averaged over 30 independent model runs.

traits are set to 0, the model is nonevolutionary and stock dynamics are driven solely by ecological processes including density-dependent growth. Larger CVs enable a stronger contribution from fisheries-induced evolution (22). Using the fishing mortalities estimated for NEA cod for 1932–2006 (*S1. Model Description* and *Fig. S14*), we analyze how the model's capacity to match the observed maturation trends varies with these CVs (Table 1 and *Table S1*).

Although eco-evolutionary models have been used to investigate fisheries-induced evolution, the present study is unique because of its tight coupling of long-term time series data for a wild fish stock with the retrospective simulation of the stock's dynamics based on a carefully calibrated model; this is a different approach from other, more strategic or general, models of life history evolution (22, 23, 51, 57). Crucially, we let the data “decide” on the most plausible levels of evolution, by determining which values of CV maximize the fit (measured through the likelihood function) between the model and the data.

Results

When using the historical growth model (describing weak density dependence), the nonevolutionary model with all four CVs set to 0 predicts stock collapse (i.e., population extinction) around 1980, which obviously did not happen in reality (*Fig. 1 A* and *B*). Even when considering an alternative maturation schedule (obtained by pooling the PMRNs of cohorts from 1932 to 2005, which results in higher survival, earlier maturation, and the avoidance of stock collapse in the nonevolutionary model), the match with the empirical maturation trends remains very poor when evolution is absent and the historical growth model is used (*S4. Alternative Maturation Model*, *Fig. S2*, and *Table S2*). In contrast, the best (likelihood maximizing) evolutionary model variant when using the historical growth model reproduces the observed trends in age and length at maturation well (*Fig. 1 A* and *B*). These findings support the hypothesis that trait evolution has contributed to the stock's dynamics during the 20th century, assuming that the historic density-dependent growth relationship is accurate.

When using the contemporary growth model (describing strong density dependence), a model variant with low CVs performs best (by likelihood), suggesting that, for this growth model, a good match with the data can be achieved with little fisheries-induced evolution (*Fig. 1 C* and *D*). This is possible because with stronger density dependence, fishing results in significantly faster growth, which in turn promotes significantly earlier maturation

Table 1. Top-ranked model variants with their CVs for the four considered life history traits (i, PMRN intercept; g, growth capacity; GSI, gonadosomatic index; s, PMRN slope)

CV _i	CV			Log-likelihood, ln L	AIC difference
	CV _s	CV _g	CV _{GSI}		
<i>i</i>) Historical density-dependent growth model					
0.02	0.06	0.14	0.02	-177.74*	1.7
<i>0.02</i>	<i>0</i>	<i>0.14</i>	<i>0.08</i>	-177.88	0
<i>ii</i>) Contemporary density-dependent growth model					
0.02	0.1	0.04	0.12	-181.22*	2.9
<i>0.02</i>	<i>0</i>	<i>0</i>	<i>0</i>	-182.75	0

Two alternative density-dependent growth models are considered: (*i*) the historical growth model and (*ii*) the contemporary growth model. The models are ranked by their log-likelihood ln L (higher is better) and AIC relative to the model variant with the lowest AIC (lower is better). For each growth model, the best-fitting model variants are shown (in bold for the maximum likelihood and in italics for the lowest AIC). For an extended version of this table, see *Table S1*.

*Having maximum likelihoods, these model variants are shown in *Fig. 1*.

via phenotypic plasticity. This greater scope for growth-related maturation plasticity means that less evolution is required to explain the observed maturation trends.

The top-ranked model variants are similar when evaluated using the Akaike information criterion (AIC), which combines a measure of fit to the data (likelihood) with a penalty (58) for each positive CV (Table 1). In these model variants, the CVs for the two maturation traits are consistently low (0% or 2%), and this also applies to the CVs for reproductive investment (0–4%), regardless of the applied growth model (Table 1). In the top-ranked model variants, the CVs for growth are consistently high (14%) when the historical growth model is used, but consistently low (0–4%) when the contemporary growth model is used (Table 1). This occurs because more growth evolution is required to match the observed maturation trends when the density dependence of growth is weak. For the top-ranked evolutionary model variants, we can thus conclude as follows. First, the PMRN intercept shows a slow and steady evolutionary decline from 1950 onward, because selection from the feeding-ground fishery favors earlier maturation (*Fig. S3A*). Second, the PMRN slope and GSI evolve very little, with the GSI showing a tendency to increase over time (Table 1 and *Fig. S3 B* and *C*). Third, growth capacity evolves more quickly, particularly when the historical growth model is used (*Fig. S3D*).

Although the model variants are selected solely based on matching the empirical time series of age and length at maturation, they perform well in predicting the empirical time series of other stock characteristics, including length at age (*Fig. S4*), phenotypic growth rate (*Fig. S5A*), and recruitment at age 3 y (*Fig. S5B*). However, although the overall qualitative trends are similar, the total stock biomass estimated from a stock assessment model consistently exceeds that predicted by our model (*Fig. S5C* and *S6. Comparison with Other Observed Trends*).

Also, our model generally matches the spawning stock biomass estimated from the stock assessment model during the earlier part of the time series, but less well in recent years (*Fig. S5D*).

Discussion

The world's largest cod stock, NEA cod, was recently reported to be at the highest biomass levels ever recorded (59). Other fish stocks, like those of northern cod around Newfoundland, have collapsed due to, among other factors, high fishing pressure (60, 61). However, although NEA cod has historically also experienced high fishing pressures, with a mean fishing probability of 49% per year from 1932 to 2006 (27), it has persisted and even thrived. There are likely multiple reasons for the continued success of the NEA cod fishery, but the predictions of our model suggest, in the case of weakly density-dependent growth, that evolution has contributed to preventing stock collapse and sustaining the substantial fishing pressure the stock has experienced. However, our analyses show that density-dependent growth is also critically important for interpreting the observed trends in life history traits and stock dynamics. This is highlighted by how predictions differ depending on whether the density dependence of growth is assumed to be strong or weak. When growth is strongly density dependent (i.e., for the contemporary growth model), the performance of the nonevolutionary model and best-fitting evolutionary model variants are statistically similar. Even though some of the tested evolutionary model variants fit the data better (i.e., had a higher likelihood and a lower AIC) than the corresponding nonevolutionary model, the AIC difference of 0.6 between the nonevolutionary model and the evolutionary model variant with lowest AIC is small (and in this case, only one CV was positive, yet small) (Table 1). It is generally accepted that all models within an AIC difference of 2 of the best-fitting model have similar empirical support (e.g., ref. 58).

Several other predictions are sensitive to the growth model used (Table 1 and *Fig. S1B*). Most importantly, stock collapse

(i.e., population extinction) is predicted when the density dependence in growth is assumed to be as weak as that estimated for the historical period and there is no concurrent evolution. Furthermore, the historical growth model predicts much more growth evolution than the contemporary growth model (Fig. S3D). The reason is that the historical trends in age and length at maturation can partly be explained by increased phenotypic growth, which can arise in two ways: growth is strongly density dependent (so the reduction in biomass from fishing enables faster phenotypic growth) or growth evolves to be faster. Therefore, the best-fitting model variants have a high CV of growth if growth is weakly density dependent or a low CV of growth if growth is strongly density dependent.

Although it is not possible to determine with certainty which growth model is more accurate, the weight of evidence suggests that the contemporary growth model is more reliable. The contemporary growth model has a high explanatory power and enables a superior fit to the observed trends in length at age (especially for older ages; Fig. S4), supporting a model with strongly density-dependent growth and less growth evolution. Importantly, the quality of the data used to estimate the contemporary growth model is higher and additional environmental variables could be accounted for (S1. Model Description), lending good empirical support to this model and providing evidence for more strongly density-dependent growth. However, aquaculture studies of Atlantic cod (62, 63) suggest a high genetic variance in growth, and previous studies of other species found evidence for harvest-induced evolution of growth (10, 29, 64, 65), suggesting that weaker density dependence and more evolution of growth are possible. Another possibility is that the strength of density-dependent growth has varied over time, which could happen if, for example, ecosystem conditions have changed (66, 67).

Our analyses reveal less fisheries-induced evolution in NEA cod than previous studies of this and other marine fish stocks (3, 8, 35, 68). In particular, our model variants with higher CVs of the maturation traits produce poorer matches with the time series data. This could indicate a large contribution from phenotypic plasticity in explaining historical dynamics in NEA cod, with less contribution from evolutionary change than previously thought (28, 35, 50, 51). As a result of lower CVs, PMRN evolution predicted by our top-ranking model variants is considerably slower and smaller in magnitude than predicted by other eco-evolutionary models (22–24, 55). However, those previous models were not specific to NEA cod; for example, two of these models were for a generic Atlantic cod stock (22, 23) and one was for smallmouth bass (55). When examining CVs similar to those assumed in these previous models, we also predict more PMRN evolution; but by comparing with empirical data, these higher rates of evolution result in unrealistically low ages and lengths at maturation for this stock (27) (Fig. S6). The overall magnitude of change in the PMRN found in our study is also smaller than what has been previously inferred for NEA cod (35), as well as for other fish stocks (8, 65, 68–70). It is only by statistically matching our model predictions with empirical trends under different scenarios of density dependence that we come to these different conclusions about the likely magnitude of fisheries-induced evolution in NEA cod.

The reasons why previous empirical estimates of PMRN dynamics differ from our model-predicted PMRN trends are unclear. However, we can point out several key assumptions that may contribute. First, the PMRNs of individuals are genetic traits in our model, whereas empirical estimates of PMRNs are based on phenotypic data, which themselves are subject to measurement error (including unaccounted environmental effects) and other assumptions (11). Second, we assume linear PMRNs, whereas empirically estimated PMRNs can be nonlinear. Because PMRNs can often be estimated only for a few ages, robust extrapolation of their shapes beyond the empirically well-covered age range is not

possible, hampering the identification of nonlinearities in their shapes. Nevertheless, the nonlinearities of empirically estimated cod PMRNs are not strong (9, 34, 35) and are therefore unlikely to have a large impact on maturation dynamics. Third, increasing the CVs of the PMRN intercept and slope—in our current model implementation—widens the population-level PMRN, and thereby enables earlier maturation. An alternative way of implementing increases in these two CVs is to simultaneously reduce the individual-level variability in maturation, such that the population-level variability remains unchanged (S7. Higher Genetic Variances). This could favor higher CVs of the PMRN intercept and slope among the best-fitting model variants and result in better agreement with the estimated PMRN trends, offering an interesting challenge for future research (S8. Model Limitations).

Our model predicts the evolution of increased growth capacity, a finding that might seem unexpected given earlier experiments (29, 71, 72) but is in agreement with model-based studies (22, 23, 40, 73) and theory (39). A closer look reveals a logical explanation for faster growth. In most fish, growing faster causes maturation earlier in life. By evolving a higher growth capacity, individuals can thus mature earlier, with a higher probability of reproducing before being caught by the fishery. Such a response is expected to occur when the fishery's minimum-size limit is low enough that both immature and mature fish are harvested (22, 40), as is the case for NEA cod in the feeding grounds. By allowing growth capacity to evolve and by including phenotypic plasticity in maturation, we capture this selection pressure. Our model predictions are strengthened by their good match with data on length at age (Fig. S4) and on phenotypic growth (Fig. S5A). For NEA cod, phenotypic trends toward faster somatic growth (implying larger lengths at age) have indeed been documented for older age groups (74, 75). The recognition that model-predicted maturation evolution is altered by growth evolution strengthens the case for including multiple evolving traits in life history models.

Although our model predicts a genetically based increase in reproductive investment (GSI), the magnitude of this evolutionary change is so small that it would be difficult to detect in the wild. This finding is in accordance with empirical data: liver weight (standardized for body length) in NEA cod, a possible proxy of the energy available for reproduction (76), exhibited no more than a weak overall increase from 1946 to 2001 (75). Furthermore, no consistent temporal trends in reproductive investment have been detected (77), and as far as we know, no other empirical data published to date suggest genetically based changes in reproductive investment in NEA cod. Previous eco-evolutionary models have also predicted less fisheries-induced evolution of reproductive investment than for PMRNs or growth (22).

Although our eco-evolutionary model is not the only one to address density-dependent growth simultaneously with life history evolution (24, 47, 57, 78), it quantitatively links model results to life history changes that have unfolded in a wild fish population as it was harvested. By mimicking the observed annual fishing mortalities experienced by this stock (Fig. S1A), we are capturing underlying interactions between the resource and human behavior, as the historical fishing pattern is the outcome of how humans (e.g., fishers, managers, and society), among other factors, have interacted with the stock as it changed over time. This is an added dimension that, although important, is typically neglected in most biological models used to predict trends in exploited populations and is another reason why tight coupling with empirical data is so powerful.

The model we present succeeds in capturing important aspects of the NEA cod stock's response to harvest, highlighting the necessity of including key feedbacks between ecology and evolution. For example, the evolution of growth, often left out of models of fisheries-induced evolution, plays a prominent role in matching stock dynamics because of its interaction with maturation and

reproduction. We conclude that it is the simultaneous consideration of ecological and evolutionary dynamics that is required to explain the full breadth of observed trends. By using an empirically grounded eco-evolutionary life history model of NEA cod, we have shown that, although some evolution is needed to prevent stock collapse and therefore sustain harvest, density-dependent growth could account for much of the maturation change observed in this stock. Our approach serves as an example of how the tight coupling of a calibrated eco-evolutionary model with empirical time series data can be used as a tool for designing sustainable harvest regimes as part of an integrated approach to ecosystem-based management.

Materials and Methods

Our eco-evolutionary model describes the life cycle of NEA cod. It is built upon the model framework described by ref. 22, and a full description of the model can be found in ref. 27. We therefore only focus on key elements below and provide additional details in the *S1. Model Description*. The model is eco-genetic, containing ecological and genetic details that describe key features of an individual's life cycle, including birth and inheritance, growth of soma and gonads, sexual maturation, reproduction, and natural and fishing mortality. It is empirically based and has multiple evolving life history traits that are expressed phenotypically, allowing for environmental variation and phenotypic plasticity to influence observed trait values. We model differential mortality regimes experienced by the stock in spawning and feeding grounds, but include no other spatial structure. The model is defined by statistical relationships and parameter values derived from empirical data available for NEA cod, including time series of fishing mortalities, density-dependent growth, and recruitment from 1932 to 2006.

Our model describes quantitative inheritance and evolution of four life history traits: somatic growth capacity, reproductive investment (measured by the GSI), and the intercept and slope of the PMRN. Offspring inherit genetic trait values from their parents assuming normally distributed genetic variation around the midparental values (with the corresponding variance for each genetic trait equaling one-half of its genetic variance in the initial population), describing the effects of recombination, segregation, and mutation (22, 27). The genetic trait values are expressed by drawing normally distributed phenotypic trait values with variances that equal the interindividual environmental variance estimated for each trait. Interannual environmental variation is included in the model through density-dependent growth. Genotypes that better enable survival and reproduction will be selected for over time, changing the stock's trait distributions. Emergent trait phenotypes of special interest are the age and length at maturation. If the genetic trait values affecting these phenotypic traits change over time, trends in the stock's mean age and length at maturation have an evolutionary component.

Phenotypic plasticity occurs when a genotype is expressed as different phenotypes as a function of the environment (79). We include phenotypic plasticity in our model through density-dependent growth and PMRNs. Density-dependent growth is included to account for the expected increase in per capita resource availability as population biomass is reduced by fishing (59). Density-dependent growth has been observed in many species, including marine fish stocks (80), and our parameter estimation using time series data provides empirical support that it also occurs in NEA cod (*S1. Model Description*). In our model, an individual's phenotypically expressed growth

rate is determined by reducing its genetic growth capacity as a function of population biomass. As phenotypic growth rates change with population biomass, the age and length at maturation shift along the PMRN (11).

The derivation of parameter values is fully described in ref. 27, with the most pertinent details highlighted here (all model parameters are listed in the *S2. Model Parameterization*). The initial population-level mean trait values for the genetic traits are estimated from empirical data; the resultant genetic trait distributions of individuals in the population are then free to change through time depending on selection. A unique feature of this study is the comparison between two different density-dependent growth models, the parameters of which are determined empirically (*S1. Model Description*). For the historical growth model, we assume a relationship estimated from data for 1932–1950. As fishing mortalities were lower during this time and because of the averaging that is inherent in estimating this model, the density dependence of growth inferred for this period is weaker. For the contemporary growth model, we assume a relationship estimated from data for 1978–2009. The density dependence of growth inferred for this contemporary period is stronger. To mimic the fishing pressure experienced by the stock, we use data on the annual fishing mortalities in the feeding grounds and spawning grounds from 1932 to 2005 (*S1. Model Description*).

The CV of a trait directly influences the rate of evolution and is equal to the genetic SD of the trait divided by the trait's mean value (22, 55, 81, 82). To evaluate models with alternative rates of evolution, we vary the CV of each of the four traits in the initial population (24) independently from 0% to 14% in steps of 2% (ideally, optimization should be performed over the whole continuous range of CV values; restriction to a discrete set of values was chosen due to computational costs). Thus, $2^4 = 16$ model variants are analyzed (resulting from choosing a zero or positive CV value for each of the four traits) based on $8^4 = 4,096$ CV combinations (resulting from considering eight CV values for each of the four traits). Consequently, one model variant and one CV combination describe stock dynamics without any evolution (i.e., with all four CVs equaling zero), whereas all others correspond to evolution being possible in at least one of the traits. Each CV combination is run for 30 independent replicates (resulting in a total of $4,096 \times 30 = 122,880$ model runs) and their results are averaged for that CV combination. The performances of all model variants and associated CV combinations are statistically evaluated, using the likelihood function and the AIC, by comparing model predictions for annual mean ages and lengths at maturation with 74 y of observations on maturation in NEA cod (*S3. Model Selection*).

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