LETTER

Nine decades of decreasing phenotypic variability in Atlantic cod

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Abstract

Changes in phenotypic variability in natural populations have received little attention in comparison with changes in mean trait values. This is unfortunate because trait diversity may influence adaptive evolutionary change and population stability. We combine two unique data sets to illuminate complex trait changes in Atlantic cod along the Norwegian Skagerrak coast: (i) an annual beach seine survey starting in 1919, monitoring juvenile body size and abundance and (ii) capture–mark–recapture data from which we estimated selection on juvenile body size and growth. We demonstrate that the variability of juvenile size has been steadily decreasing across nine decades, with no evidence for a similar trend in mean size. We also report that small, slow-growing fish as well as large, fast-growing fish are selected against. Together, these results suggest long-term stabilizing selection acting on Atlantic cod, and emphasize the need for further studies evaluating the full complexity of trait changes in wild populations.

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INTRODUCTION

There has been a rash of recent studies demonstrating contemporary phenotypic changes in wild populations (Hendry & Kinnison 1999; Hendry *et al.* 2008; Darimont *et al.* 2009). Such changes are not limited to human-influenced populations, although human activities do appear to precipitate greater changes than more natural contexts (Hendry *et al.* 2008; Darimont *et al.* 2009). The majority of these studies have focused on detecting changes in *mean* trait values, that is, change driven by directional selection. Changes in trait *variability*, or those driven by nonlinear (e.g. stabilizing or disruptive) selection, are also likely but have received less attention (but see Handford *et al.* 1977; Hutchings & Rowe 2008; Haugen *et al.* 2008). This is unfortunate because changes in trait variability have consequences for the adaptive potential of wild populations (Allendorf *et al.* 2008), as well as population stability and resilience to environmental change (Hilborn *et al.* 2003; Anderson *et al.* 2008; Stenseth & Rouyer 2008).

Changes in trait variability could occur through a variety of mechanisms including changing fitness landscapes due to varying environmental conditions or trans-generational plastic effects (e.g. maternal effects). Changes in trait variability could also be driven by human activities. For example, Carlson *et al.* (2007) reported consistent disruptive selection acting on a harvested fish population across four decades. Despite evidence of nonlinear natural selection (reviewed in Kingsolver *et al.* 2001) and nonlinear anthropogenic selection (e.g. fishery selection, Carlson *et al.* 2007), changes in phenotypic variability are rarely evaluated.

Herein, we test for evidence of complex trait changes in Atlantic cod (*Gadus morhua* Linnaeus) collected along Norway's Skagerrak coast (Fig. 1). The Skagerrak coastal cod have been the subject of scientific inquiry for nearly one century. Across this time span, data on juvenile cod abundance and body size have been collected through a highly standardized beach seine survey, together with information on environmental parameters such as sea surface temperature (Stenseth *et al.* 1999). Here, we combine these long-term data with more recent capture–mark–recapture data collected on coastal cod from the same region (Danielssen & Gjøsæter 1994). The semi-enclosed nature of the study system and the non-migratory behaviour of these coastal cod allowed multiple recaptures and releases of many tagged individuals. We used the former dataset to
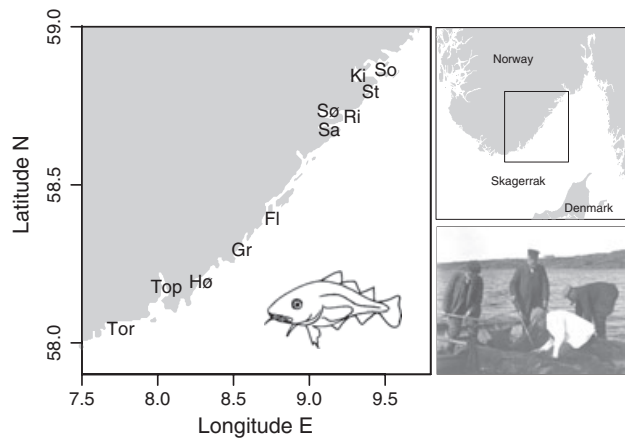
Figure 1 Coastal cod sampled from the Norwegian Skagerrak coast through a beach seine survey and a capture–mark–recapture study. The beach seine stations were distributed over 11 areas: Torvefjorden (Tor), Topdalsfjorden (Top), Høvåg (Hø), Grimstad (Gr), Flødevigen (Fl), Sandnesfjorden (Sa), Søndeledfjorden (Sø), Risør (Ri), Stølefjorden (St), Kilsfjorden (Ki) and Soppkilen (So). The capture–mark–recapture study was conducted in two areas: Søndeledfjorden (Sø) and Risør (Ri). Historical photo shows GM Dannevig (centre), who initiated the beach seine survey in 1919.

quantify phenotypic changes in juvenile cod across the past nine decades and the latter dataset to estimate the strength and form of contemporary selection acting on combinations of cod body size and growth. By doing so, we specifically test whether the long-term phenotypic changes are consistent with the observed selection operating on this marine fish.

Using the long-term beach seine data set, we demonstrate a nine-decade decrease in the variability of juvenile cod body length. In contrast with earlier research, we report no long-term change in mean body length. Using a recent capture–mark–recapture data set, we also show that contemporary selection acted against large and fast-growing as well as small and slow-growing juvenile cod. The correspondence between the two data sets suggests consistent stabilizing selection acting on juvenile cod body size across the last nine decades. These results suggest the need to expand our vision and methods for assessing phenotypic change in wild populations.

MATERIALS AND METHODS

The Skagerrak coastal cod

The Atlantic cod is a commercially important marine fish found in coastal waters and offshore shelf habitats in the North Atlantic Ocean. Offshore populations are often characterized by long-distance migrations linked to feeding and spawning, while coastal populations, e.g. along Norway's Skagerrak coast, tend to be more spatially confined (Knutsen *et al.* 2003; Espeland *et al.* 2008). Compared with many other cod stocks, coastal Skagerrak cod have a

relatively short life cycle. Annual survival probabilities are often below 0.5, and few fish live beyond 5 or 6 years of age (Olsen *et al.* 2004a). A significant proportion of the fish mature at an age of two years and a body length of 30–35 cm (Olsen *et al.* 2008). Spawning occurs in sheltered fjord basins, mainly during the months of March and April (Knutsen *et al.* 2007). The Atlantic cod is a highly fecund and iteroparous batch spawner with pelagic eggs and larvae (Kjesbu 1989). In Skagerrak, the age 0 juveniles settle in shallow water nursery areas during May and June. There is evidence that these nursery areas also receive an influx of juveniles from cod spawning offshore in the North Sea (Stenseth *et al.* 2006). Skagerrak cod are harvested year-around by both commercial and recreational fishers using a range of gear (Julliard *et al.* 2001). The minimal legal size is currently 40 cm, although this regulation only applies for commercial harvest. The recruitment of Skagerrak coastal cod has varied considerably during the last century, and there is evidence for density-dependent juvenile survival linked to competition and cannibalism (Stenseth *et al.* 1999). Density-dependence has also been inferred from length-distributions of juvenile fish, where skewness tends to increase with increasing population density (Lekve *et al.* 2002). Harbour seals (*Phoca vitulina* L.) and great cormorants (*Phalacrocorax carbo* L.) are potential predators, but little is known about their impacts.

Beach seine data

A beach seine survey has been conducted annually since 1919 during the months of September and October, providing nine decades of research data on abundance and body length of juvenile cod along the Norwegian Skagerrak coast (Fig. 1; for details, see Stenseth *et al.* 1999). During the war years (1940–1944), only two stations were sampled and so these years were excluded from our analyses. The current survey includes *c.* 130 stations. Here, we have included only those stations that have been sampled during at least 90% of the study years (*n* = 31 stations, 43 932 cod).

Before 1960, all captured cod were measured for length. After 1960, a random subsample of 100 individuals was measured for length in those cases when more than 100 cod were captured in a single haul. In total, 41 989 individuals were measured for length. There is little overlap in length between age 0 cod and older cod, facilitating age assignment of the youngest fish. We used a length–frequency analysis to objectively disentangle age 0 fish from the total catch length data (see Appendix S1, Table S1 and Fig. S1). The resulting estimates of mean and standard deviation of age 0 length were used as response variables in ordinary least squares (OLS) regression analyses, testing for a temporal trend in body length. Through a model comparison approach, we also tested the importance of sea surface temperature and

cod density (Fig. 2), estimated as mean cod catch per haul, for explaining interannual variation in age 0 cod body length. Sea surface temperature was based on daily observations at 1 m depth in the bay outside the Flødevigen Research Station during July–September, when most of the age 0 cod will have completed their pelagic larval stage and settled in shallow, near-shore nursery habitats.

Capture–mark–recapture data

A capture–mark–recapture study was conducted during 1988–1992 (Fig. 1; for details, see Danielssen & Gjøsæter 1994). Wild cod were hatched and reared in captivity and then individually tagged and released as half-year olds (age 0 fish) during October and November. The fate of the tagged fish was studied mainly through a survey using eel-traps that were set in the shallow waters of the fjord system. This study design allowed for multiple observations on individual cod, because recaptured fish were usually in good condition and released alive back into the study system. The survey was conducted in collaboration with local eel-fishers, who tend to catch a substantial number of cod as bycatch in their eel-traps. The eel-fishers were paid to register and release any tagged cod. Additional data were provided from recreational and commercial fishers reporting captures of tagged cod.

Julliard *et al.* (2001) previously used this data set to analyse age-specific survival. Here, we build on this earlier work by analysing the size- and growth-specific survival of those fish that were trapped and released back into the system (live recaptures) at some point during their second year of life (i.e. age 1 cod), providing individual-based observations on age 0 size, age 1 size, as well as the number of days in the sea and the distance moved between these capture events (see Appendix S2, Fig. S2). A total of 672 individuals fulfilled these criteria, of which 17.1% ($n = 115$) were seen again at 2 years of age or later in life. Growth during the age 0 to age 1 time interval was estimated for each fish as the residual from

an OLS regression of $\log_e L_1$ on $\log_e L_0$, where L_0 was the body length at age 0 and L_1 the body length at age 1. We also included the time (days) each fish spent in the sea between initial release and first recapture as a covariate in this regression since fish were recaptured throughout their second year of life (age 1). Previously, this approach was used to estimate selection on relative growth in juvenile brown trout (*Salmo trutta* L.), and the main idea is to quantify each individual's growth *relative* to that of similar-sized conspesifics (for details, see Carlson *et al.* 2004). Specifically, individuals with positive residuals will have grown faster than predicted based on their initial length and time spent in the sea, while individuals with negative residuals will have grown more slowly than predicted. Details on this regression model can be found in Appendix S2, Table S2.

We next used program MARK (White & Burnham 1999) to explore if and how selection operated on combinations of juvenile cod size and growth rate. This software computes maximum likelihood estimates of ϕ, the apparent survival probability, and P, the recapture probability, where both ϕ and P may be functions of individual covariates such as body size, growth, and dispersal distance. A major advantage of this approach over traditional approaches for estimating selection (i.e. Lande & Arnold 1983) is that survival estimates are unbiased by variation in recapture probability (see also Gregoire *et al.* 2004; Carlson *et al.* 2008; Marquis *et al.* 2008). Apparent survival represents the combined probability that an animal survives from capture occasion i to capture occasion $i + 1$ and is available for recapture at capture occasion $i + 1$.

The Cormack–Jolly–Seber model (Lebreton *et al.* 1992) served as a starting point for the analyses. This model allows both survival and recapture probabilities to vary with time for a single group of animals, and was used for goodness-of-fit testing (for a similar example, see Marquis *et al.* 2008). The global test in program U-CARE (Choquet *et al.* 2005) indicated that the Cormack–Jolly–Seber model fitted the data reasonably well (d.f. = 3, $\chi^2 = 2.53$, P-value = 0.47),
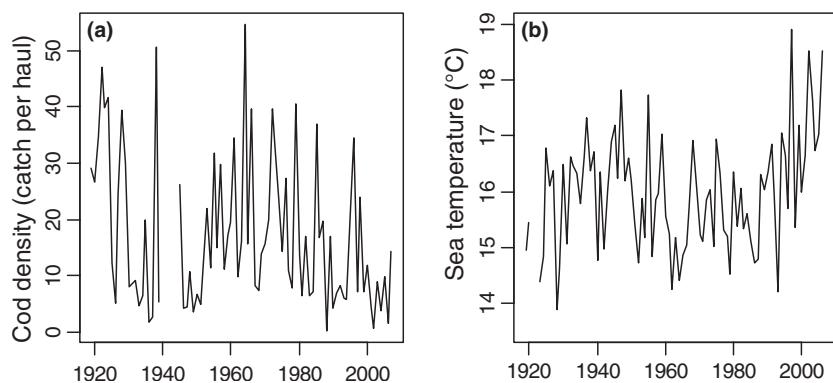
Figure 2 Ecological conditions in coastal Skagerrak from 1919 to 2007 including (a) mean density of coastal cod estimated as mean catch per beach seine haul and (b) mean sea surface temperature (°C) during the summer growing period.

and this model therefore served as a starting point for our survival analyses. Model selection was based on AIC_C, i.e. the Akaike Information Criterion corrected for small sample bias (Burnham & Anderson 1998). We first defined the most parsimonious structure describing variability in recapture probabilities and then used this structure to model survival. In program MARK, the survival and recapture parameters were expressed as linear functions of covariates using the logit link (White & Burnham 1999), e.g. survival may be given as:

$$\phi = e^{\beta 0 + \beta 1 size + \beta 2 growth + \beta 3 size \times growth} \Big/$$
$$1 + e^{\beta 0 + \beta 1 size + \beta 2 growth + \beta 3 size \times growth},$$

where β_0 is the intercept and β_{1-3} are the slope parameters for effects of size and growth. All covariates were standardized to a mean of zero and a SD of unity. Using standardized input variables, these slope parameters will allow for a direct comparison with estimates of selection from earlier studies. Specifically, the cross product term (size × growth) estimates the *bivariate quadratic selection gradient*, which can be interpreted as favouring similar traits (e.g. large size and fast growth) when positive and dissimilar traits (e.g. small size and fast growth) when negative. For comparison, we also estimated the *linear selection differentials* on size and growth rates from simpler models containing only one of the two covariates. These coefficients represent the total strength of selection acting on either trait, possibly involving both direct selection on the trait in question as well as indirect selection as a result of correlation with other traits. We also tested for effects of body size, growth rate, and dispersal distance on the probability of recapture because we expected that large size and fast growth would lead to a higher probability of recapture because of gear selectivity and because larger individuals may have a more bold behaviour (Biro & Post 2008). We also expected that long-distance dispersal would lead to a lower recapture probability, because local eel-fishers would be more informed and motivated to report recaptures compared with fishers outside of the central study area.

The recapture data included both live recaptures released from eel-traps and also fish captured in other gear, such as gillnets, by recreational and commercial fishers not directly involved in the study. While it is possible to run models in MARK which incorporate information on both live recaptures and dead recoveries, preliminary analyses using this approach revealed problems of parameter identifiability because of a sparse number of dead recoveries ($n = 80$). Instead, we coded all fish as censored (removed from the study) on last capture if not captured and released from an eel pot (i.e. if captured via some other method). For comparison, we analysed the probability of being harvested (i.e. captured in gear other than eel-pots), using a traditional logistic regression approach for estimating harvest-induced selection (Carlson *et al.* 2007), testing for effects of age 0 body size, growth during the age 0 to age 1 interval, and dispersal distance during the same interval.

RESULTS

Long-term phenotypic change

The long-term beach seine data did not indicate any long-term trend in the *mean* body length of age 0 cod over the past nine decades (Fig. 3a), but did indicate a clear trend of reduced *variability* in body length (Fig. 3b). Statistical comparison of linear models based on AIC confirmed these observations. Considering temporal variation in mean age 0 cod length, the model capturing the most support included only a single covariate – *mean sea surface temperature* during the growing season (AIC = 203.2). Moreover, the only other model within 2 AIC units of the best model also included a temperature effect (*cod density + mean sea surface temperature*, AIC = 204.2), providing further support for the importance of temperature over the first growing season to inter-annual variation in age 0 cod body length. Despite the consistency of these results, *mean sea surface temperature* was not a significant predictor of average age 0 cod length (*P*-value = 0.714).

Considering temporal variation in the standard deviation of age 0 body length, the model capturing the most support included both *cod density* and *year* (Table 1, model 6, AIC = 128.4), with a statistically significant effect of *year* (slope = −0.0081, SE = 0.0022, *P*-value < 0.001) and a marginally significant effect of *cod density* (slope = −0.0082, SE = 0.0044, *P*-value = 0.066). Two other models were within 2 AIC units of the best model and both of these also included *year* as a covariate (Table 1: *cod density × year*, model 7, AIC = 128.6; *year*, model 5, AIC = 129.9) providing further support for a temporal trend in the standard deviation of age 0 cod body length.

Contemporary selection

Modelling of capture–mark–recapture data on juvenile cod from the same region showed that both survival and recapture probability (i.e. live recaptures in eel pots) depended on individual phenotypes. Specifically, the model receiving the most support contained an interaction between body size (at age 0) and growth rate (from age 0 to age 1 year) on future survival, and additive effects of dispersal tendency and body size on future recapture probability (Table 2, model 4). Models containing an additive effect of body size and growth on survival, or a single effect of body size, also received some support (Table 2, models 6 and 7).
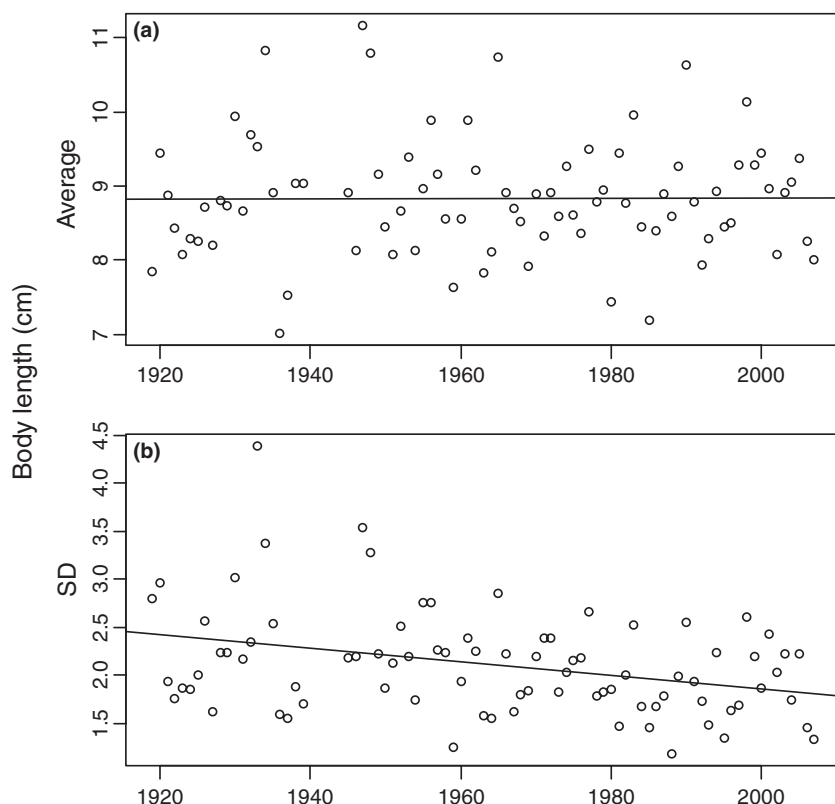
Figure 3 Long-term trends in (a) mean body length and (b) standard deviation of body length of age 0 Skagerrak coastal cod sampled in a beach seine survey from 1919 to 2007.

Table 1 Model selection for estimating a temporal trend (Year) in the standard deviation of cod body length (SDlength) and the influence of environmental covariates: mean annual cod catch per beach seine haul (Catch) and mean summer sea temperature (SST)

Model number	Model structure	AIC
6	SDlength = Catch + Year	128.4
7	SDlength = Catch × Year	128.6
5	SDlength = Year	129.9
2	SDlength = SST	138.2
1	SDlength = Catch	139.3
3	SDlength = Catch + SST	139.8
4	SDlength = Catch × SST	141.5

This was also true for a model including an additive effect of growth on recapture probability (Table 2, model 5). Other candidate models received only marginal support (Table 2). The model that received the most support (i.e. model 4) suggests that individuals dispersing relatively far from the site of initial release during the juvenile stage had a lower probability of being recaptured later in life as compared with more stationary individuals ($\beta_{dispersal} = -0.55$, SE = 0.20). Also, fish that were smaller at age 0 tended to have a lower probability of future recapture as compared with larger individuals ($\beta_{size} = 0.56$, SE = 0.26). The overall mean

probability of recapture in a given year was 0.39 (SE = 0.06).

The data supported a nonlinear effect of juvenile growth and size combined on future survival, although the confidence interval was not clearly distanced from zero ($\beta_{size \times growth} = -0.21$, SE = 0.13). This became clear, however, when we used the same model structure to test for an effect of age 1 body length (rather than age 0 length) on survival from age 1 and onwards ($\beta_{size \times growth} = -0.33$, SE = 0.12). Selection acted against small fish that grew relatively slowly from age 0 to age 1 (small size and slow growth). Selection also acted against large fish that grew fast from age 0 to age 1 (large size and fast growth). On the other hand, selection strongly favoured small fish that grew rapidly from age 0 to age 1 (small size and fast growth). Fish having an intermediate size and growing at intermediate rates were also predicted to have relatively high survival probability (Fig. 4). For comparison, linear selection differentials (Table 2, models 7 and 8) indicated a weak negative total selection for body size at age 0 ($\beta_{size} = -0.34$, SE = 0.16) and age 1 ($\beta_{size} = -0.21$, SE = 0.21), and a weak positive total selection for growth ($\beta_{growth} = 0.16$, SE = 0.11). Thus, these data suggest stabilizing selection acting on combinations of juvenile body size and growth. Note that we also analysed the capture–mark–recapture data using observed growth (cm day^{-1}, see Appendix S2, Fig. S2)

Table 2 Model selection for estimating juvenile cod survival (ϕ) and recapture probabilities (P) from tagging data, showing the AIC_C score and the support (AIC_C weight) in favour of each candidate model

| Model number	Model structure	AIC_C	Support
The Cormack–Jolly–Seber model			
1	ϕ_{time}, P_{time}	786.6	0.00
Modelling recapture probabilities			
2	$\phi_{size \times growth}$, $P_{constant}$	787.3	0.00
3	$\phi_{size \times growth}$, $P_{dispersal}$	780.3	0.06
4	$\phi_{size \times growth}$, $P_{dispersal + size}$	777.5	0.25
5	$\phi_{size \times growth}$, $P_{dispersal + size + growth}$	777.8	0.22
Modelling survival probabilities			
6	$\phi_{size + growth}$, $P_{dispersal + size}$	778.3	0.17
7	ϕ_{size}, $P_{dispersal + size}$	778.0	0.19
8	ϕ_{growth}, $P_{dispersal + size}$	780.5	0.06
9	$\phi_{constant}$, $P_{dispersal + size}$	780.6	0.05
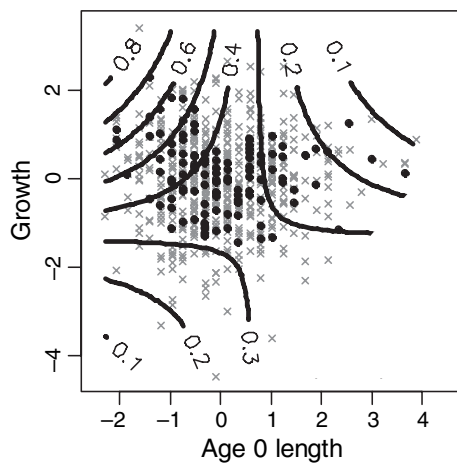
Figure 4 Selection acting on combinations body size and growth in juvenile cod. Contours represent annual survival probabilities as predicted from capture–mark–recapture modelling of tagged fish (Table 2). Size is standardized body length (see Materials and Methods) at an age of *c.* 8 months (age 0). Growth is standardized relative increase in length (cm) from age 0 to age 1 (see Materials and Methods). Field observations are shown separately for those fish that were never recaptured after being released at age 1 (✕) and those that were recaptured at some point later in life, i.e., the known survivors (●).

rather than relative growth as an explanatory variable. This second approach also suggested that large fast-growing cod as well as small slow-growing cod were selected against (results not shown).

We found no evidence for an effect of either body size or growth on the probability of being harvested when using a standard logistic regression approach (*P*-value > 0.2), although there was a marginally significant negative effect of dispersal distance on the probability of being harvested (*P*-value = 0.10). Detailed results can be found in Appendix S2, Table S3.

DISCUSSION

This study demonstrates a nine-decade decrease in the variability in body length of juvenile Atlantic cod and an equally long-lasting absence of change in the mean body length. Moreover, we show that contemporary selection acted against large and fast-growing as well as small and slow-growing juvenile cod. The long-term decrease in variability of body length and the concurrent absence of change in mean body length strongly suggests the presence of stabilizing selection acting on juvenile cod body size across the last nine decades. This result contrasts the many studies documenting changes in *mean* trait values in wild populations (e.g. Hendry & Kinnison 1999) and suggests the need for further work evaluating approaches for capturing the full complexity of trait changes in wild populations.

Does the long-term change in Skagerrak cod trait variability reflect evolution or phenotypic plasticity? The results suggest some evolutionary component to the change because the patterns in the beach seine data are consistent with the observed selection where both large and fast-growing fish as well as small and slow-growing fish are strongly selected against. Also, juvenile growth is known to be a heritable trait in Atlantic cod (Gjerde *et al.* 2004), meaning that it can evolve in response to selection. We note that the high survival predicted for small, fast-growing fish also suggests some directional selection for small body size at age 0, provided that compensatory growth can be obtained at a later stage. However, we interpret this latter result with caution because data are sparse for combinations of rapid growth and small size.

Possible causes of complex trait changes

There are several non-exclusive mechanisms by which complex trait changes in coastal Skagerrak cod could arise. First, a long-term trend in climatic conditions could drive

the observed changes, but the available data on sea surface temperatures in the region suggest no consistent long-term trend over the period of record. Interestingly, we did find weak evidence of a positive effect of summer temperature on *mean* cod length, suggesting that local environmental conditions drive short-term fluctuations in this trait and, thus, the potential for future longer-term trends in temperature to drive changes in this aspect of size. This result is consistent with earlier work that has documented interannual variation in the direction and magnitude of selection, which drives rapid evolution in opposite directions over contemporary time frames (Grant & Grant 2002). As a consequence, the rate of phenotypic change generally tends to be higher for short-term studies as compared with long-term studies, the latter smoothing out short-term fluctuations (Hendry & Kinnison 1999).

Second, long-term trends in biotic parameters including density of conspecifics, predators, or prey could also drive the observed trait changes. In juvenile cod, for example, interannual variation in population density might influence phenotypic variability via size-dependent mortality driven by cannibalism or competition for resources such as high-quality patches of nursery habitats (Tupper & Boutilier 1995; Stenseth *et al.* 1999; Lekve *et al.* 2002). Here, we report that density of conspecifics had a negative impact on the variability in age 0 cod length but there was no apparent long-term trend in juvenile cod density (Fig. 2), which suggests that this factor did not account for the long-term trend in phenotypic variability. However, this observation does suggest that density-dependent selection (Reznick *et al.* 2002) is operating in this system, wherein selection is relaxed (i.e. diversity increased) when population density is low and vice versa.

Third, changes in breeding phenology could drive the observed trait changes. Specifically, a shift in the timing and duration of the spawning season might influence both the mean size and the variability in size of age 0 cod captured in the beach seine because these factors determine the time available for growth between hatching and capture. Specifically, a contracted breeding period will lead to a contracted hatching period, which will presumably result in less variability in the age (in days since hatching) and size of the resulting juveniles. Unfortunately, we do not have any direct information on temporal trends in the timing or duration of the spawning and hatching seasons. Given the lack of a long-term temporal trend in sea surface temperature, we suspect that spawning period has not changed in a consistent direction over the period of record.

Fourth, natural selection could be driving the observed changes. The capture–mark–recapture data strongly suggest that selection on combinations of body size and growth rates is ongoing. Both the smallest and the largest juveniles were selected against, that is, contemporary selection is stabilizing. Moreover, large-fast growing individuals were selected against, while intermediate to small-fast growing fish were favoured, suggesting some evidence of a compensatory ('catch up') strategy. For comparison, Gagliano & McCormick (2007) found that the surviving juveniles of a coral reef fish (*Pomacentrus amboinensis* Bleeker) were those that initially grew relatively slowly, during the early settlement phase on the reef, but then shifted towards a period of accelerated (i.e. compensatory) growth. It seems plausible that selection favouring individuals with specific combinations of trait values could result in decreased (small-fast growing and large-slow growing) or increased (small-slow growing and large-fast growing) trait variability through time. We note that environmentally induced covariance between phenotypes and fitness can lead to biased estimates of natural selection (Kruuk *et al.* 2003). For instance, micro-scale variation in the quality of nursery habitats is likely to influence growth and survival of juvenile cod (Tupper & Boutilier 1995). In this study, tagged cod were raised in a common environment, thus reducing the initial environmental influence on variability in size. Additionally, because the initial release of fish was randomized with respect to body size (the fish were released in batches along the shores of the fjord), this should essentially have prevented any covariance between initial phenotype (or genotype) and environment. We therefore believe that we have presented a robust analysis of selection acting on combinations of cod body size and growth.

Finally, we note that each annual length distribution consists of pooled data from 31 stations. Thus, annual variation in the pooled length-distributions used for analyses could be influenced by annual variation in the relative contribution from different localities. It was not possible to analyse site-specific length distributions because of small sample size at individual sampling sites (see Fig. 2). Nevertheless, we consider the pooled sample to be an appropriate measure of the phenotypic variability in juvenile cod along the Skagerrak coast because the samples were collected from a standardized set of stations and the sampling procedure has also remained highly standardized (see also Stenseth *et al.* 1999). Furthermore, all stations are found within *c.* 150 km of coastline, thereby excluding any large-scale biotic and abiotic effects.

Potential role of harvest

Given several recent studies showing ecological and evolutionary effects of harvesting on the Atlantic cod (e.g. Olsen *et al.* 2004b; Swain *et al.* 2007), it is plausible that harvest may have played a role in driving trait changes. Harvesting typically leads to age- and size-truncation of the parent stock, which may reduce the phenotypic variation of offspring because of: (i) the positive relationship between

offspring size and maternal size (e.g. Trippel 1998) and (ii) a more restricted spawning period (Hutchings & Myers 1993) leading to less variation in age (and size) of juveniles. Unfortunately, the adult coastal cod in Skagerrak have not been monitored in any consistent manner over the time period covered by the beach seine survey, which targets juvenile fish. Age and length data collected sporadically back to the early 1900s suggest no long-term increase in fishing pressure in this region across the last century. In fact, age- and length-distributions were apparently more skewed towards small and young spawners a century ago relative to more recent data (Dahl & Dannevig 1906; Olsen *et al.* 2008).

Propagule subsidies from the North Sea cod population, a heavily harvested population, could also play a role. Recent population genetic data have revealed that juvenile cod in coastal Skagerrak are actually a mixture of local coastal cod and an influx of larvae from the North Sea (Stenseth *et al.* 2006). Earlier research has demonstrated that the Skagerrak beach seine data contains a North Sea abundance signal – i.e. that the abundance of juvenile cod in coastal Skagerrak is increased in years when the spawning biomass of oceanic North Sea cod is high and the ocean currents are favourable for transport (Stenseth *et al.* 2006). Therefore, it is possible that overfishing and collapse of the North Sea cod during recent decades (Cook *et al.* 1997) may have influenced the phenotypic diversity of juveniles rearing in the Skagerrak, along with stabilizing local selection pressures operating on juvenile cod. Both processes might co-occur, but our data set specifically supports the latter explanation while we have no direct observations supporting the former (North Sea influence). Hence, our discussion focuses mainly on the coastal selection regime.

The capture–mark–recapture data primarily reflect natural selection because harvested fish were censored from the analyses. Thus, in our analyses, a recapture indicates that the focal individual survived a given episode of selection. However, tag reporting rates were probably no higher than 60% (Julliard *et al.* 2001), meaning that our survival estimates are, to some degree, influenced by harvesting (i.e. fish are disappearing because they are harvested but not reported). Importantly, the recapture parameter (i.e. the probability of being captured given that the fish is still alive and available for capture) also provides some information about harvest selection. Specifically, the positive effect of body size on the probability of being recaptured supports earlier studies, showing that fishing often selects larger individuals (e.g. Kristiansen & Svåsand 1998; Carlson *et al.* 2007; Swain *et al.* 2007). However, the regression analysis on fish harvested outside the survey (i.e. killed by commercial and recreational fishers) did not support any effects of body size on the probability of being harvested. While this could be related to the overall scarcity of such recoveries, it could also simply mean that the harvesting regime in this coastal region is not particularly size-selective. The fact that Skagerrak cod are harvested by both commercial and recreational fishers using a wide variety of gear (Julliard *et al.* 2001) provides some support for this assertion.

Implications

This study has implications for the management of harvested species because the level of phenotypic (and genetic) diversity will influence a population's future adaptive potential and resiliency to future environmental change (Hilborn *et al.* 2003; Allendorf *et al.* 2008; Anderson *et al.* 2008). This study also sheds light on the potential impact of domesticated marine fish on their wild conspecifics. In Norway, the Atlantic cod is considered the most promising new marine species for the aquaculture industry, with more than 500 commercial farming licenses currently issued (Jørstad *et al.* 2008), and with good prospects for 'genetic improvement' of growth rate (Gjerde *et al.* 2004). However, recent experiments have documented that farmed cod will spawn in net pens and that the eggs disperse over fairly large distances and mix with wild fish (Jørstad *et al.* 2008). Our results suggest that mixing of fast growing domesticated fish with wild cod could drive maladaptive changes in wild local populations because rapid growth and large body size are strongly selected against. We therefore caution against rapid expansion of cod aquaculture in this region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Year-specific length distributions and length–frequency analysis based on beach seine data during 1919 to 2007.

Appendix S2 Analyses of capture–mark–recapture data.

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