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Comparing rates of contemporary evolution in life-history traits for exploited fish stocks

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Abstract

Trait evolution over time periods spanning generations, not millennia, is increasingly observed to be above the natural baseline in populations experiencing human-induced perturbations. We investigated the relative speed of trait change by comparing rates of evolution in haldanes and darwins for primarily size at maturation as measured by probabilistic maturation reaction norm midpoints for fish stocks from the Pacific, North Atlantic, Barents Sea, Eastern Baltic, and the North Sea. Rates in haldanes for 23 stocks ranged from -2.2–0.9 and from 0.5–153 in kdarwins for 26 stocks. The highest rates of evolution corresponded to the most heavily exploited stocks; rates slowed after moratoria were introduced. The estimated rates in fish life-history characteristics were comparable to other examples of human-induced evolution, and faster than naturally-induced rates. Stocks with high growth showed slower evolutionary change, even under high mortality, suggesting that compensatory somatic growth can slow the rate of trait evolution. Regardless of whether trait changes are due to exploitation or environmental factors, the costs of ignoring trait evolution are high. As management strategies should be based upon precautionary principles, the effect of changing traits must be integrated into the fisheries assessment process.

Keywords: contemporary evolution, darwins, fisheries-induced evolution, haldanes, life-history traits, probabilistic maturation reaction norms

Running title: Rates of evolution in marine fish stocks

INTRODUCTION

A wide range of life-history strategies have evolved to maximize life-time reproductive success under current environmental conditions (Stearns 1992; Hendry and Gonzalez 2008; Lande 2009). Organisms can become maladapted to their environment as a result of naturally occurring change; individuals must then either adapt to the new environment through phenotypic plasticity or evolution, or decline and face extinction (Hendry and Gonzalez 2008; Hendry et al. 2011). Because background environmental variation is typically not characterized by dramatic or abrupt changes, strong natural selection tends be uncommon (Kingsolver et al. 2001), thus, the adaptation process is regarded as being relatively slow under natural variation. However, rapid or contemporary evolution, defined as significant trait evolution in less than a few hundred generations (Hendry and Kinnison 1999), is increasingly observed. Examples include populations adapting to natural or anthropogenic environmental variation, but the principal factor capable of imposing such a strong selective force appears to be humans (Palumbi 2001; Mace and Purvis 2008; Hendry et al. 2011). Anthropogenic disturbances often occur rapidly and include novel stressors thereby necessitating swift, although often unpredictable, responses (Mace and Purvis 2008; Crispo et al. 2010). Hendry et al. (2008) found that rates of phenotypic trait change from anthropogenic disturbances were nearly double those from natural environmental perturbations. The selective force on traits is thought to be especially strong if it arises from hunting or harvesting (Darimont et al. 2009) due to the immediate selection for a particular trait, such as large size or large antlers and horns, coupled with a demographic effect (Coltman et al. 2003; Allendorf and Hard 2009; Hendry et al. 2011). Phenotypic changes from harvesting were found to be greater than natural and other anthropogenic disturbances by factors of 3.4 and 1.5, respectively (Darimont et al. 2009).

A number of studies have shown that exploitation is capable of inducing evolutionary changes in behaviour, morphology, and life-history characteristics when the selected phenotype has a partial genetic basis for large mammals (Coltman et al. 2003; Proaktor et al. 2007) and fish (reviewed by Law 2007; Dunlop et al. 2009; Sharpe and Hendry 2009). Exploited fish stocks typically show truncated size and age distributions (Longhurst 2002; Hutchings and Baum 2005; Hsieh et al. 2010) as a direct consequence of increased mortality, facilitated by the size-selective nature of most fisheries, where the likelihood of capture increases with size. Intensive harvesting, whether size-selective or not, tends to favour genotypes with earlier maturation (Law and Grey 1989; Allendorf and Hard 2009) and may have unforeseen consequences for the entire community (Jennings and Kaiser 1998; Heino and Godø 2002; Coltman et al. 2003). Sustainable exploitation depends upon sustaining yield over time, yet harvesting of only those individuals with desirable traits, such as large size, creates an unnatural selection that is at odds with sustainability (Jørgensen et al. 2007; Coltman 2008; Allendorf and Hard 2009). Changes in yield and productivity can be linked back to changes in life-history traits, such as growth rate, length and age at maturation, and fecundity (Law and Grey 1989; Conover and Munch 2002; Stergiou 2002). Although evolutionary changes may be reversible, the long and impractical time frames needed for reversal are not at the appropriate scale for current management policies (de Roos et al. 2006; Conover et al. 2009; Enberg et al. 2009). Andersen and Brander (2009) suggested that fisheries-induced evolution is too slow to warrant attention by managers, but management should be concerned if the rate of change is fast, i.e., on the scale of years or few decades as opposed to over hundreds of years (e.g., Law 2007).

Is fisheries-induced evolution fast? To measure and compare the rate of change between traits and species, quantitative measures of evolutionary rates are needed. Evolutionary rates, especially when assessing the speed of trait change for fish populations (e.g., Jørgensen et al.

2007; Sharpe and Hendry 2009), have typically been quantified in darwins (Haldane 1949). The darwin represents the relative rate of change on an absolute time scale (in units of *e* per million years) and is useful when measuring change that is relevant to time-dependent human interests (Hendry and Kinnison 1999). The ease of estimation is its foremost advantage. However, the darwin was not developed for quantifying rates of contemporary evolution; the intended application was for long temporal scales, i.e., morphological traits from the fossil record (Hendry and Kinnison 1999; Roopnarine 2003). Furthermore, the darwin is influenced by trait dimensionality; rate comparisons between populations with different generation times can be misleading, and it is useful solely for ratio scale data, where the scale has a precise zero point corresponding to a null quantity (Gingerich 1993; Hendry and Kinnison 1999).

More recently, haldanes (Gingerich 1993) have been proposed as a metric for quantifying evolutionary rates. Unlike the darwin, haldanes are applicable to both ratio and interval scale data (where the zero point is arbitrary), are more widely comparable and, more importantly, are on the time scale over which evolution takes place (i.e., the generation time of an organism; Gingerich 1993; Hendry and Kinnison 1999; Gingerich 2001). The haldane was proposed to estimate the change in a population trait in units of standard deviation per generation (Gingerich 1993); haldanes scale the magnitude of change by the amount of variation in the trait. Describing the rate of change over generations, rather than years, is preferable when estimating the intensity of selection or to understand how a particular trait responds to environmental changes because it is using a time scale relevant to the life history of the organism (Gingerich 1993; Hendry and Kinnison 1999). Haldane estimation requires knowledge of the phenotypic variation of the trait of interest and generation time of the organism, both of which can be difficult to estimate, hence their lack of use when assessing rates of fisheries-induced evolution. Haldanes and darwins, although correlated (Hendry and Kinnison 1999), are not the same; darwins retain some dimension-dependency (Gingerich

1993). However, comparisons of the two metrics should provide insight into common evolutionary patterns because .. (Gingerich 2001; Kinnison and Hendry 2001).

Rates in haldanes can be scaled to a timescale of one generation, first referred to as an intrinsic rate of evolution (Gingerich 1993) and later revised to generational rate (h_0) (Gingerich 2001). Generational rates are the relative amount of variation within a population between successive generations and are proposed to be directly comparable with rates predicted by evolutionary theory; rates per generation on a timescale of one generation (Gingerich 1993; 2009). Although generational rates are useful for assessing the amount of change, they should not be used as an indication of selection (Gingerich 1993).

Here we assess the relative speed of fisheries-induced trait change by estimating contemporary rates of evolution in haldanes and darwins for length at maturation from probabilistic maturation reaction norm (PMRN) midpoints. PMRNs aid in disentangling the effect of phenotypic plasticity from genetic effects on maturation (Heino et al. 2002; Heino and Dieckmann 2008) and have been used to investigate changes in age and size at maturation for many fish stocks (e.g., see references in Table 1). PMRNs, by describing the probability of becoming mature as a function of age and size, are thought to remove the main effects of varying mortality and juvenile growth rates (Dieckmann and Heino 2007). However, this approach does have limitations; PMRNs have been criticized for failing to disentangle all effects of growth from maturation (Morita and Fukuwaka 2006; Heino and Dieckmann 2008; Morita et al. 2009) and for not accounting for factors other than growth-related phenotypic plasticity in maturation (Dieckmann and Heino 2007; Wright 2007; Uusi-Heikkilä et al. 2011). Furthermore, temperature appears to partially account for the trends in maturation probability. Some studies have attempted to address this by including the effects of condition and temperature on the maturation process, through the use of higher-dimensional PMRNs (Baulier et al. 2006; Grift et al. 2007; Mollet et al. 2007; Vainikka et al.

2009), by incorporating other factors directly into the maturation reaction norm estimation (Devine and Heino 2011; Wright et al. 2011a; Wright et al. 2011b), or through experimental manipulation (Tobin and Wright 2011). Molecular genetic methods have yet to confirm the evolutionary nature of these changes, but the overriding conclusion of many of the maturation reaction norm studies was that phenotypic changes likely had a genetic component.

Several review papers have used PMRN data to assess rates in darwins (Jørgensen et al. 2007; Darimont et al. 2009; Sharpe and Hendry 2009), but the difficulty in estimating phenotypic standard deviation has hampered assessment in haldanes. The haldane rates we estimate are new for most stocks (Olsen et al. (2004) has previously estimated haldanes describing fisheries-induced evolution), and this is the first comparative study to utilize haldane rates in our context. Here, we estimate evolutionary rates for twenty-six fish stocks, mainly gadoids and flatfish, from the Pacific, North Atlantic, Barents Sea, Eastern Baltic, and the North Sea. Many of these stocks currently support fisheries, while others have been under moratorium for almost two decades. We assessed whether (1) putative fisheries-induced evolution qualifies as being fast using two rate metrics, the easily-calculated darwins and the more refined haldanes, (2) a deterministic pattern is apparent in the evolutionary trajectory of haldane rates, and (3) the speed of evolution can be correlated with total mortality and somatic growth.

METHODS

Data collection

Data were included in the analysis if they met the following criteria: 1) were from a probabilistic maturation reaction norm study, 2) included a time series of PMRN midpoints (L_{p50}, the size at 50% maturation probability), 3) included either the quantiles (e.g., the sizes at which the probability of maturing is 25% and 75%), or , if estimated using the direct

PMRN method (Heino et al. 2002), the length-slope of the logistic regression, and 4) if data were not readily available from the literature, could be obtained directly from the authors (Table 1). If multiple PMRN studies were available for the same stock, the best available data were used e.g., those that corresponded to the longest time period. Focusing only on PMRN studies allowed for comprehensive coverage of all available literature, including studies that showed both increasing and decreasing trends in length at maturation. Because the PMRN method disentangles a large proportion of the contribution of variation in growth and mortality from other sources of variation involved in the maturation process (Dieckmann and Heino 2007), albeit with some criticisms (see above), PMRNs are less confounded by non-evolutionary factors than other traits, such as size at 50% maturity (not to be confused with the PMRN midpoint), which are sensitive to fluctuations in demography and the environment. Consequently, rates estimated from PMRN studies could be expected to be higher than rates for traits that retain environmental variability.

Environmental factors may directly affect the maturation process even after growth and mortality variation are accounted for in the PMRN estimation (Tobin and Wright 2011), but this effect can be partially removed with higher-dimensional PMRNs or by including covariates directly in the reaction norm estimation (Kraak 2007). We chose to use only data from two-dimensional PMRNs to facilitate comparison with rates estimated from the numerous other lower-dimensional PMRN studies, but included two studies that explicitly investigated the effect of environmental factors, Barents Sea haddock (*Melanogrammus aeglefinus*, Gadidae) and Northeast Arctic cod (*Gadus morhua*, Gadidae) (Table 1). Rates were expected to differ when compared with those estimated from traditional PMRNs. The PMRN method was marginally different for these two populations, but the use of the haldane for stock comparisons, as opposed to the darwin, should minimize any issues that arise due to variation in how the trait was measured (Hendry and Kinnison 1999).

Time series should be examined for shifts in trait evolution when selective pressure significantly changes (Hendry and Kinnison 1999). As moratoria reflect abrupt change in fishing intensity, rates were estimated separately for pre- and post-moratoria periods for several Northwest Atlantic cod stocks and chum salmon *Oncorhynchus keta*, Salmonidae).

Evolutionary rates

Darwins (d) were estimated as:

(1) $$d = \frac{\ln(x_1/x_0)}{\Delta t \times 10^{-6}},$$

where x_0 and x_1 were back-transformed values estimated for the beginning and end of the time series from linear regression on $\log_e$-transformed trait data over time, and Δt was the number of years in the time series (Haldane 1949). Logarithmic transformations were used because data were geometric normal (Gingerich 2000). A change of one darwin means that the trait would change by a factor e in one million years.

Haldanes (h), the rate of change in standard deviations per generation, were estimated using the procedure outlined by Gingerich (1993), with correction by Hendry and Kinnison (1999) as:

(2) $$h = \frac{(x_1 - x_0)/s_p}{g},$$

which is simply the change in the trait over the time period, divided by the product of the pooled phenotypic standard deviation (s_p) and the number of generations (g) spanning the time period. As with darwins, the start and end points of the trait change (x_0 and x_1) were generated from linear regression of $\log_e$-transformed trait data over time, back-transformed into original units.

The phenotypic standard deviation (s_P) can be calculated from the width of the probabilistic maturation envelope around reaction norm midpoints (Olsen et al. 2004), treating the midpoint as a threshold trait with a certain population mean and variance (Bulmer and Bull 1982; Gianola 1982; Wesselingh and de Jong 1995). The width of the envelope is related to the degree to which uncontrolled factors cause apparently stochastic variation in maturation tendency and, when estimated at the population level, genetic variability in the reaction norms of individuals (Olsen et al. 2004; Heino and Dieckmann 2008). When the reaction norm is described by the logistic curve, the standard deviation of the reaction norm midpoint is the standard deviation of the corresponding logistic distribution. The standard deviation from PMRNs estimated with the direct method using logistic regression (Heino et al. 2002; Heino and Dieckmann 2008) is:

(3) $$s_p = \frac{\pi}{\sqrt{3}\beta_s},$$

where β_s is the length (size) coefficient of the reaction norm model (Metcalf et al. 2003). If the length coefficient is unknown or PMRNs were estimated with the demographic method (Barot et al. 2004a; Heino and Dieckmann 2008), the length coefficient can be calculated from the width as $\beta_s = \lfloor \mathrm{logit}(p_{upper}) - \mathrm{logit}(p_{lower}) \rfloor / w_{p_{lower}, p_{upper}}$, where $w_{p_{lower}, p_{upper}}$ is the width, i.e., the distance between sizes with maturation probability p_{lower} and p_{upper} (commonly 25% and 75%). For the demographic method, this is an approximation because the PMRN does not exactly correspond to the shape of a logistic curve.

Generation time is the average age of the mothers of newborn individuals and, for iteroparous life histories, is always greater than the age at maturation. Because fecundity is often highly correlated with weight in fish, generation time could be approximated using the following equation:

(4) $$t_g \approx \frac{\sum_{t}^{t_{\max}} t \times S_t \times M_t \times W_t}{\sum_{t}^{t_{\max}} S_t \times M_t \times W_t},$$

where t_g is generation time, t_{max} is maximum age, S_t is numbers-at-age t, M_t is the maturity ogive, and W_t is the average weight-at-age t. Maturity ogives describe the proportion of individuals mature at a given size or age and are not to be confused with PMRN midpoints. Data for maturity ogives, and numbers- and weights-at-age were taken from ICES, NAFO, or DFO stock assessment reports (Table 1). Generation time was calculated for all analysed years?/cohorts?, and the geometric mean corresponding to the time period of the PMRN study was used to calculate the Haldane estimate., but a range of values were investigated to test the effect of underestimating generation time on the haldane estimates.

We used the LRI analysis (log-rate versus log-interval; Gingerich 2001; 2009) to assess whether evolutionary rates in length at maturation could be considered random, directional, or stationary. Gingerich (1993) showed that the slope from a log-rate versus log-interval (LRI) relationship, where rates were estimated over multiple time intervals (e.g., over one generation, 2-generations, 3-generations), could be used to indicate stasis or stabilizing processes (slope = -1.0), randomness (slope = -0.5) or directional change (slope = 0). Rates within our dataset were not strictly independent, i.e. rates were from males and females and different age cohorts in the same stock. To reduce non-independence, one rate for each stock should be chosen, however, the decision of which age or sex to use would likely be arbitrary. We used an alternative way of dealing with non-independence and pseudoreplication: we used a linear mixed effects model (LME) to test the relationship between absolute rate in haldanes and the number of generations (time interval), and included stock + period (all, pre- or post-moratorium) as a random intercept term, and assumed a Gaussian distribution for the error term. The random intercept term implies that the estimated evolutionary rates for each age class and sex within a single stock (or subpopulation) were most likely correlated. Absolute rates were used because the direction of change was not relevant in comparing the relative speed between stocks. Absolute values may artificially inflate the observed change as a result of measurement error, however, the bias is small if the contribution of measurement error is similar for all indices (Hendry and Gonzalez 2008) or if the estimated slope is significantly different from zero (Hereford et al. 2004). Generational rates (h_0) were estimated from the intercept of the regression of $\log_{10}$-rate on $\log_{10}$-interval (Gingerich 2009). Parameters were bootstrapped to obtain 95% confidence intervals. This analysis was not performed for darwins because the LRI method assesses trait change on a generational basis. All LME models were fit in R (R Development Core Team 2011), using the lme4 package (Bates et al. 2011).

Evolutionary rates are not independent of the time interval over which they are measured. Short timescales tend to capture dramatic changes, whereby the initial response to a perturbation is large and fast and slows with increasing time after the disturbance (Reznick et al. 1997; Kinnison and Hendry 2001; Hendry et al. 2008). This decline with increasing time is an artefact of the negative self-correlation caused when rates that have time in the denominator are compared with time (Sheets and Mitchell 2001). The importance of this self-correlation was investigated in two ways: 1) by randomizing the rate numerator (trait difference) with respect to the denominator and inspecting the correlation of the randomized rate versus the original rate estimate, and 2) by inspecting the numerator or the rate estimate against time interval. Randomizing the numerator and re-estimating rates should eliminate the correlation, but a strong negative correlation approximating the actual pattern is often still apparent (Sheets and Mitchell 2001). If significant autocorrelation within the data exists, the underlying trend can nevertheless still be examined by testing if the slope and intercept differ from those estimated from the randomizations (Kinnison and Hendry 2001). Analysing the haldane numerator ($(x_1–x_0)/s_p$), which is the total phenotypic change in multiples of phenotypic standard deviation, removes time from the rate estimation, thereby circumventing some of the intrinsic self-correlation; rates of phenotypic change can then be compared against time. When analyzing phenotypic change, untransformed data are typically used, but the untransformed data here indicated heteroscedasticity. Since violation of this assumption has the greatest bias on p-values, transformed data were used, but $\log_{10}$-transformed data tend to be influenced by short time intervals (Kinnison and Hendry 2001; Hendry et al. 2008). Both the average and maximum absolute phenotypic change for a particular sex-stock-trait combination was used as an estimate of the average and maximum amount of change that might be accomplished. The use of one value per sex and stock avoided most of the non-independence issues of using multiple data points within a system. Because we chose to include data on both sexes within a stock, LME models were again used with a unique stock + period identifier as a random intercept term and a Gaussian distribution for the error term.

Mortality and growth rates

Total mortality rates (Z, year^{-1}), were used to investigate the relationship between rates of evolution and all sources of mortality in the environment. Total mortality includes the direct effect of fishing (Beverton and Holt 1957), unaccounted mortality, such as that from escape and discard mortalities, and other unknown mortalities (e.g., predation), which are often reflected as part of the natural mortality component (Chopin et al. 1996). Rates were estimated from the change in abundance with age for each year class, using data gathered from stock assessment reports (Table 1). We did not quantify size dependence of fishing or total mortality, but we note that management of all fish stocks in our study includes minimum landing size or minimum mesh size regulations. The mortality regime of the previous generation will affect life-history traits in the current generation. Therefore, a lag was introduced by including mean mortality rates up to one generation before the end of the trait time period, i.e., for North Sea sole, change in maturation was estimated for cohorts 1964–1996 and generation time was 3.8 years, therefore, mean mortality from 1960–1992 was used. For stocks under moratoria, the lag in total mortality was one generation after enactment of the moratorium.

Mortality estimates for several of the Northwest Atlantic cod stocks (2J, 3K, 3L, and 3Ps) did not include a long pre-moratorium time series. Abundance data were not available prior to the 1983 year class, although catch numbers at age did exist from which catch curve analysis could be used to estimate total mortality. Using estimates from catch curve analysis was not ideal because data were only for the combined stocks, which could have resulted in over- or underestimation of *Z* for individual stocks. Additionally, the assumption of constant catchability, recruitment, and mortality over age and time (Ricker 1975) has been shown to be somewhat inaccurate for Northern cod (Atkinson et al. 1997). Estimates from the catch curve analysis were substituted only when no estimates of total mortality were available from abundance data.

Catch curve data for combined northern cod stocks 2J3KL had to be used to estimate total mortality for stock 3L after 1996 as Z estimated from the abundance data was 0.1 yr^{-1}; the low value was deemed highly unlikely and so a mean Z of 0.51 yr^{-1} was used. Catch curve data were also used to estimate mortality for the post-moratorium period for cod stock 3K and prior to the 1983 cohort for 3Ps due to lack of abundance data for those cohorts. Mortality rates for Southern Gulf of St Lawrence cod post-moratorium cohorts were generated from Swain et al. (2009) as the sum of fishing mortality and natural mortality, where natural mortality was estimated from models.

Because growth rate can affect other traits, such as survivorship, age at maturity, and reproductive output (Stearns 1992; Law 2007; Waples and Naish 2009), and variation in growth may be a reflection of variation in the abiotic and biotic environment, it was used as an indicator of stock productivity. Growth rates may vary as a result of density-dependence or environmentally driven changes in individual growth (Trippel 1995). Growth rate was estimated from the Gompertz growth curve:

(5) $$W(t) = W_\infty \exp\left[-\frac{\lambda}{K} e^{-Kt}\right],$$

where $W(t)$ is weight at age t, taken from stock assessment reports (Table 1), W_∞ is asymptotic weight, λ is the initial relative growth rate when $t = 0$, and K (year^{-1}) is the relative growth rate at the inflection point. The Gompertz growth model is an alternative sigmoidal growth curve, which can be used to describe mean growth of individuals or growth of populations (Quinn and Deriso 1999) and was used here as it fit the data for several stocks and cohorts better than the von Bertalanffy model. Therefore, for consistency, the Gompertz growth model was used for all stocks and year classes. Growth rates were averaged over cohorts corresponding to the PMRN data used in the haldane and darwin rate estimation.

A generalized additive mixed model (GAMM; Wood 2006) was used to investigate the relationship between evolutionary rates (*r*), total mortality (*Z*), and growth (*K*), where predictor variables were fit with spline functions. Differences in body shape (i.e., flatfishes) or life-history (e.g., iteroparous vs. semelparous) might confound model results; therefore the analysis was restricted to one family, Gadidae (here represented by cod and haddock). GAMMs included a Gaussian error distribution, an identity link, and a unique stock + period random intercept term, as defined for LME models. The full model was first fitted using an interaction term, but it appeared to overfit the data and the AIC was greater than the model with no interaction term. A log link was inspected, but the identity link better described the relationship between predictor and response variables. GAMMs were fit in R (R Development Core Team 2011) using the gamm4 package (Wood 2011).

RESULTS

Evolutionary rates

Evolutionary rates in haldanes for 23 stocks, including subpopulations and pre-/post-moratorium periods, and kdarwins (10^3 darwins) for 26 stocks ranged from -2.2 to 0.9 and from 0.5 to 153, respectively (see supplemental tables for rates by sex and age for each stock). The distributions of absolute rates were skewed; the majority of rates were slow and only a few were very fast (Figure 1). Generally, the pre-moratorium Northwest Atlantic cod stocks showed the fastest rates of change, whereas post-moratorium cod stocks, North Sea plaice, and North Sea sole exhibited the slowest rates (Table 1, Figure 2). Rates for chum salmon after the closure of the high seas gillnet fishery were faster than rates pre-closure, indicating that size at maturation was evolving towards larger sizes faster than it had declined. Because haldane rates estimated for less than one generation could be considered too uncertain, post-moratorium rates for two stocks, Atlantic cod 3NO and 3Ps, were omitted from the haldane analyses. Darwin estimates for these two stocks may also be suspect due to the short time interval. The number of generations for all other stocks ranged from 1.1 to 12 and the time interval ranged from 5 to 59 years (Figure 1).

Generational time may have been underestimated because most of the stocks had been exploited prior to the time of the PMRN studies. If generation time was actually greater than estimated, the rate of change will be greater than that estimated here (see supplemental table/figure). Conversely, if generation time was overestimated, our rates will be also be overestimates.

For stocks that included environmental factors as covariates within the original PMRN models, evolutionary rates were within the range exhibited by all stocks (see supplemental material). Mean rates were significantly different when comparing pre- and post-moratorium stocks (haldanes and darwins, $p < 0.001$). The pre-moratoria rates of the Northern cod stocks (2J3KL) were 60%–95% faster than post-moratoria rates. For Southern Gulf of St. Lawrence cod, the differences were less pronounced (23–28% faster than post-moratoria for males, 63–67% for females). Rates of change for weight at maturation in North Sea sole were significantly faster than for length at maturation ($p_{haldane} = 0.05$; $p_{darwins} = 0.01$). Sample size was too low to test if rates for chum salmon pre- and post-closure of the high seas gillnet fishery were significantly different, but post-closure rates were higher than pre-closure (Figure 2, Table 1).

For most stocks and sexes, relatively low rates in haldanes were coupled with lower rates in darwins, or vice versa (Pearson's correlation coefficient = 0.74, Figure 3); however, there were a few discrepancies. Haldane rates for North Sea sole length and weight at maturation were similar, but darwin rates suggested the changes in weight at maturation were at a much faster rate than those for length. For North Sea cod stocks, rates in haldanes were broadly similar, but the northeast substock-specific rates in darwins were much slower than other substocks. Also notable were the large differences for male and female post-moratorium rates for cod stocks 2J and 3K.

Using the LRI approach, the regression of log-rate on log-interval yielded a slope indicative of random change (slope = -0.68). The slope was significantly different from 0 and -1 ($p < 0.001$), indicating neither directional change nor stasis was taking place (Figure 2). However, the bootstrapped (bias corrected) 95% confidence interval was wide (-0.91, -0.48). The predicted generational rate (h_0) of the haldane was 0.56, with a confidence interval ranging from 0.41 to 0.87.

The inverse relationship between rates and time interval was clear (Figure 2). Correlations between the $\log_{10}$ rate and $\log_{10}$ interval for the data were significant for both haldanes and darwins ($r_{haldane} = -0.42$; $r_{darwin} = -0.28$; $p < 0.001$ for both), indicating rates were negatively correlated with the length of time over which they were measured. Rate numerators were randomized with respect to denominators (time interval) to inspect the autocorrelation pattern (Figure 2). Correlations between the rate and interval for the randomized data were significant ($r_{\text{haldane}} = -0.46$, $r_{\text{darwin}} = -0.51$, $p < 0.0001$ for both), indicating high autocorrelation still remained within the data. The underlying trend was assessed by examining whether the slope and intercept from the actual data differed from those estimated from a large number of randomizations. For rates in both haldanes and darwins, the slopes estimated from the data were significantly flatter ($p < 0.001$) and the intercepts smaller ($p < 0.001$) than those estimated from 1000 randomizations, indicating that shorter time intervals were associated with small amounts of trait change.

Slopes from linear mixed effects models of $\log_{10}$-transformed mean and maximum phenotypic change (rate numerator) over time interval were significantly different from 0 for darwins, as indicated by their confidence intervals, but not for haldanes (Table 2). For haldanes, the amount of phenotypic change might be substantial, but the distribution of the changes was similar at short and long time intervals. Darwins, however, indicated a trend towards larger evolutionary differences over longer temporal periods.

Total mortality and growth rates

Rates of trait evolution in gadoids increased with increasing mortality and decreased with increasing growth rates for haldanes, whereas only mortality had a significant effect on darwins (Table 3). Fast haldane rates were apparent even under moderate growth ($K = 0.2$ yr^{-1}) for stocks experiencing high total mortality (Figure 4). Under moderately high total mortality, haldane rates declined as growth rates increased; this effect was obvious when $Z \leq 1.0$ yr^{-1}. Rates in darwins increased with increased mortality (Figure 5).

DISCUSSION

By estimating rates of evolutionary change for life-history traits of exploited fish stocks across the North Atlantic, Barents Sea, Baltic Sea, North Sea, and Pacific, we have shown that 1) rates of evolution measured in haldanes and darwins were relatively fast, 2) generational rates were generally fast, and 3) larger phenotypic changes were apparent over longer time periods for darwins, but not for haldanes. Evolutionary rates and the amount of phenotypic change in life-history traits, namely length and weight at maturation, were similar or faster than those for species under anthropogenic disturbance published elsewhere (e.g., Hendry et al. 2008; Darimont et al. 2009; Crispo et al. 2010). Phenotypic changes due to anthropogenic change have been shown to be as high as 6–8 standard deviation units in wild populations (Hendry et al. 2008; Crispo et al. 2010), while experimental studies on small populations under strong selection have shown that the mean phenotype could be altered by several standard deviations within a relatively small number of generations (Falconer and MacKay 1996). We estimated changes as high as 14 standard deviations in wild marine fish populations under relatively high harvesting pressure, although most were typically around 2 standard deviation units. Rates estimated here may have been faster than those for anthropogenic disturbances elsewhere for two reasons. The faster rates may, in part, be a reflection of the shorter time interval over which we estimated change; a maximum time interval of 13 generations (or 73 years) as opposed to over 80 generations (or 150 years) (ref?). Dramatic changes are often captured by short timescales, where the initial response to the perturbation is large and slows with increasing time from the disturbance (Stockwell et al. 2003). Data were from PMRN studies, which dissociate some of the variability in growth and mortality from other sources of variation involved in the maturation process, whereas other rate estimates retain these influences on phenotypic expression of traits. Nevertheless, our results support earlier evidence that phenotypic change in populations associated with anthropogenic disturbance is typically faster than for those under only natural selection (Hendry et al. 2008; Darimont et al. 2009; Crispo et al. 2010).

Generational rates of 0.1 to 0.3 standard deviations per generation are considered fast when compared to the range of possible phenotypes, but not unsual (Gingerich 1993; 2009), and have contributed to the altered perception of the pace at which evolution can, and does, occur. Whether rapidity is in fact frequently encountered in nature, but not reported, has also been questioned (Hairston et al. 2005). The generational rate of change in haldanes (h0) for fish stocks presented here was 0.6 standard deviations per generation. This is in agreement with a meta-analysis of 2151 rates by Kinnison and Hendry (2001), indicating that the range reported by Gingerich (1993, 2009) may be much lower than that typically seen in populations experiencing human-induced perturbations. It is possible that our high generational rates may be a result of slight publication bias. Most of the PMRN studies investigated stocks that showed declines in size at maturation, and very few studies focused on stocks showing no or little change. If positive and negative rates are analyzed separately in the manner of Gingerich (2001), the generational rates are 0.51 and 0.54, respectively, and can still be considered high.

The amount of estimated phenotypic change increased with time, which is relatively consistent with what has been reported elsewhere for genetic studies (Schluter 2000; Kinnison and Hendry 2001), but contrary to that reported for phenotypic studies (Estes and Arnold 2007; Darimont et al. 2009; Crispo et al. 2010). The lack of a significant trend in phenotypic studies has been attributed to examining points in time across studies and traits, rather than studying temporal trends within a study or trait (Kinnison and Hendry 2001), which is what was done here. A lack of trend can also be attributed to strong selection events that rapidly deplete genetic variation, after which no further changes over time are possible. We found a significant trend in darwins, and a slightly increasing trend in haldanes, which may provide evidence that selection has not been strong enough to deplete genetic variation within these large marine fish stocks, signifying reversal in trait adaptation may be possible

(Conover et al. 2009). Genetic diversity tends to be fairly stable due to large effective population sizes even when stocks have experienced long periods of high exploitation and shifts in life-history traits (Cuveliers et al. 2011).

Variations and reversals in evolutionary trajectories are common in many examples of contemporary evolution (Gingerich 1983; Hendry and Kinnison 1999; Estes and Arnold 2007; Schoener 2011); however, the LRI application indicated that neither stasis nor directional change was occurring. This was unexpected given that we expected fisheries-induced selection to cause directional change. Non-random patterns should be apparent if directional or stabilizing selection is causing trait evolution (Gingerich 1993) and were expected to be apparent within our data given the selection caused by high exploitation. Stasis, which is a pattern of multiple reversals or high variability in rates, is thought unlikely to occur over short intervals (Gingerich 1993; 2001; Kinnison and Hendry 2001), and our failure to detect a deterministic pattern may be due to the relatively short, less than 5 generations for most stocks and never more than 13 generations, time scale of our study. Although the LRI application suggested that the rate of change in traits could not be differentiated from random change, this does not provide definite proof that the change is random. The non-significant result can be interpreted as an indication that processes are interacting to produce results that are indistinguishable from randomness, i.e. a slope approaching random change is often expected in fluctuating environments, but it can also indicate that a neutral mixture of directional and stabilizing selection processes are occurring (Roopnarine 2003; Gingerich 2009). Siepielski et al. (2009), in a meta-analysis of 5519 selection estimates from wild populations, found that strong selection is present, but rarely sustained, and change in direction is common, which will lead to evolutionary rates that appear to be under random change. Most of the included stocks have been under sustained fishing pressure, but this does not exclude the possibility that agents of selection other than fishing are also important and observable as randomness in the overall pattern. Another possibility is that the relatively short time series that dominate the analysis have made the LRI application more sensitive to measurement error in the raw data.

Rates of trait evolution in gadoids increased with increasing mortality and slowed considerably after moratoria were introduced. These results support the hypothesis that fishing provides a partial explanation for life-history evolution in exploited fish stocks. Post-moratorium stocks experienced low-mortality, high-growth environments compared to pre-moratorium stocks. Stocks with high somatic growth tended to show slower evolutionary change than those with slow growth, suggesting that compensatory somatic growth can slow the rate of trait evolution. Conover et al. (2009) showed that reversal of changes in body size was possible when high selection pressure was relaxed, but that recovery rates may be long. Our results show that while the speed of trait change slows, fish are continuing to evolve towards smaller size, and hence age, at maturation. Whether this continued trait change is an effect of exploitation or due to relaxed density dependent effects and subsequent increases in growth rate is difficult to determine. Recovery of population traits to pre-fishing conditions do not appear to be as fast as changes under high exploitation, agreement with modelling (Dunlop et al. 2009; Enberg et al. 2009) and empirical results (Conover et al. 2009).

The statistical methods currently used to explore life-history trait change, e.g., PMRNs, do not perfectly disentangle genetic effects from phenotypic plasticity due to environment (Heino and Dieckmann 2008; Morita et al. 2009; Tobin and Wright 2011). The individual phenotypic expression of traits is a function of individual genetics and environmental interactions and as such, disentangling the ecological versus genetic change is difficult to prove. Furthermore, a widely applicable method for disentangling plastic and evolutionary effects for traits other than maturation is not available. This highlights the need for indisputable evidence of genetic change. Regardless, imperfect disentanglement does not make the PMRN approach, nor the evolutionary rates estimated here, invalid.

Uncertainty in darwin or haldane estimates primarily results from errors in the estimation of the amount of elapsed time (years or number of generations), although the haldane is also sensitive to errors in the amount of change in the trait of interest or in the estimation of the phenotypic standard deviation. Accurate estimation of the number of generations is dependent upon correctly determining generation time. This is complicated by its dependence on age and size at maturation; temporal changes in these traits therefore also imply changes in the generation time. Most of the stocks included in this study have been exploited for decades to centuries, and using the geometric mean of generation time will have resulted in estimates that are less than those found in unexploited stocks. We therefore ran the risk of underestimating the rate of trait change for haldanes. If the time interval of trait change is short, errors resulting from inaccurately estimating generation time can be much larger than expected. This shortcoming means rates in darwins may actually be more accurate than haldanes in some situations (Hendry and Kinnison 1999). Hence, reporting both types of rates is generally recommended and any notable differences, such as high rates in haldanes paired with low rates in darwins, may indicate errors in the rate estimation or imply differences in trait variation with populations (i.e., substock structure was misidentified). In this study, estimates of haldanes and darwins were closely correlated for the majority of stocks, although there were a few exceptions.

We found that rates of evolutionary change are fast under high mortality, low growth regimes, but that rates slow if either growth rate increases or mortality decreases; the magnitude of change can be large if drastic measures, such as moratoria, are imposed. Fishing mortality has been shown to be responsible for changes in life history parameters, including unintentional selection for earlier maturation at a smaller size and younger age

(Andersen et al. 2007; Sharpe and Hendry 2009). Population characteristics that affect productivity and yield, such as large size, are often the traits directly selected for by humans, however, a shift towards earlier maturation will unintentionally lead to smaller average adult size and eventually to reduced yield (Law and Grey 1989; Heino 1998; Conover and Munch 2002). Management strategies typically aim to sustain yield in the short-term and including evolutionary considerations into fishery management plans, although acknowledged for decades (e.g., Stokes et al. 1993), has only recently been highlighted as essential (Jørgensen et al. 2007). Possible scenarios suggested to slow the evolutionary effects of fishing include lowering fishing mortality, enacting maximum and minimum size limits, or restricting fishing to certain areas through the use of marine protected areas or temporary closures (Baskett et al. 2005; Andersen et al. 2007; Hutchings 2009). A decrease in mortality significantly and rapidly slowed the rate of evolution in size at maturation for cod stocks in the Northwest Atlantic, and has been shown to have beneficial effects on other life history traits, such as growth and reproduction, in the short term (Rochet 1998; Andersen et al. 2007). It has been argued that the genetic effects of fishing on age and size at maturation will be slow to reverse and practically irreversible (Law and Grey 1989; Dunlop et al. 2009; Enberg et al. 2009); however, recent experimental studies have shown that the detrimental evolutionary effects of size-selective harvest can, in some cases, be overturned if sufficient genetic variation remains in the population (Conover et al. 2009). Whether this is the case for Northwest Atlantic cod stocks or if the rapid changes detected are an artefact of the short time scale is unclear. Regardless, recovery is difficult to predict without sufficient knowledge of extrinsic environmental factors capable of applying selective pressure or how these factors may influence life history characteristics under exploitation (Enberg et al. 2009).

Coltman (2008) found that even a modest exploitation rate can have a significant genetic impact on the target population when viewed on an ecological time scale. However, Hairston et al. (2005) argue that the speed of evolutionary change matters in an ecological context only if it is fast enough to alter the outcomes of ecological interactions. The effects of evolving life-history traits on population and community dynamics have been well reviewed and include modified predator-prey and competitive dynamics, amplified responses due to mutually reinforced correlations between traits, and changes in growth, condition, reproductive output and, ultimately, yield and productivity (Kuparinen and Merilä 2007; Law 2007; Coltman 2008; Hutchings and Fraser 2008). The comparable, but relatively fast, rates of contemporary evolution estimated in this study can be viewed as a positive response to the changing selection pressures imposed by decades of commercial fishing if we consider it as the ability of a stock or species to avoid extinction (Kaitala and Getz 1995; Heino 1998; Enberg et al. 2009). Given the potential for cascading negative consequences of life-history evolution on ecological time scales, there is a pressing need to determine and implement strategies that will mitigate these effects whilst maintaining sustainable fisheries and basic ecosystem services.

In conclusion, changes in life-history characteristics for exploited fish populations are occurring at a rapid rate, but have the potential to slow with increasing growth rates and declining mortality rates. Our results support the hypothesis that fishing is an important driver of life-history change in fish, in agreement with an earlier analysis by Sharpe and Hendry (2009). However, because most of the studies included here did not explicitly investigate the effect of environment on trait change (beyond the growth and survival effects accounted for by the PMRN method), we cannot rule out the possibility that the observed changes are, in part, due to environmental change. Regardless of primary causes, trait evolution is occurring and it will have repercussions for stock demographics, productivity, recovery and, ultimately, economic yield. Evolutionarily enlightened management considers both the ecological and evolutionary consequences of fishing, but fisheries management has been slow to acknowledge that characteristics of fish populations can change over time. The effect of changing traits, whether of evolutionary nature or not, has been poorly integrated into the fisheries assessment process, except in a few notable examples (e.g., Scott et al. 1999; Marshall et al. 2000; Marshall et al. 2006). By incorporating trait changes into the recruitment process, future changes in productivity can be modeled and resilience to exploitation or perturbations, such as climate change, can be explored. Furthermore, evolutionarily enlightened management needs not to be a passive observer of evolution, but could pursue strategies to slow unwanted trait evolution, for example by shifting from strategies maximizing yield towards those that protect the age and size distribution of the population.

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Table 1. Stock, time period of study (in cohorts), mean number of generations, age classes, whether environment was included as an explanatory variable in the original analysis, average absolute rates in haldanes and kdarwins for change in length (or weight) at maturation for females or both sexes combined, and direction of trend in PMRN data (decreasing or increasing). Data for the east North Sea cod stock were male-only. Where moratoria were enacted and generation time is greater than one, number of generations and evolutionary rates are given separately for pre- and post-moratorium; for chum salmon, this was pre- and post-closure of the high seas gillnet fishery. Some stocks include only the rate in darwins due to lack of data to estimate phenotypic variation. Symbols refer to those plotted in Figure 2; capital and lowercase letters refer to pre- and post-moratorium periods for cod, and filled and unfilled symbols refer to Lp_{50} and Wp_{50} rates for North Sea sole. Rates for males can be found in the Supplemental Material.

Symbol	Stock and source	Assessment reference	Time period PMRN data	Age classes	Average no. generations	Environment	Average absolute haldanes	Average absolute kdarwins	PMRN trend
Atlantic cod, *Gadus morhua*, Gadidae									
A	NE Arctic [1]	(ICES 2009b)	1946 –2005	5–10	4.6	Covariate	0.27	4.8	decrease
+	Icelandic [2]	(ICES 2010b)	1964–1999	4–8	4.7	Regression	0.06	3.8	decrease
B	Eastern Baltic [3]	(ICES 2010a)	1988–2003	2–4	3.4	–	0.28	11.9	decrease
○	North Sea [4]	(ICES 2009a)	1974–2001	2–4	7.6	–	0.25	26.2	decrease
●	S North Sea [5]	(ICES 2009a)	1976–2005	2–4	7.4	–	0.19	18.7	decrease
● , grey	NW North Sea [5]	(ICES 2009a)	1979–2005	2–4	7.0	–	0.27	25.0	decrease
0	NE North Sea [5]	(ICES 2009a)	1975–2005	2–4	8.0	–	0.12	5.0	decrease
J, j	2J [6]	(Brattey et al. 2009) and [8]	1973–2004	4–6	1.9, 2.0	–	2.20, 0.36	26.4, 10.5	decrease

K, k	3K[6]	(Brattey et al. 2009) and [8]	1973–2004	4–6	1.9, 1.9	–	1.4, 0.19	19.3, 5.0	decrease
L, l	3L[6]	(Brattey et al. 2009) and [8]	1977–2004	4–6	1.5, 1.5	–	1.87, 0.09	22.7, 1.7	decrease
N	3NO[6]	(Morgan et al. 2007) and [8]	1967–2000	5–6	2.5, –	–	0.80, –	15.0, –	decrease
P	3Ps[6]	(Brattey et al. 2008) and [8]	1967–2000	5–7	2.4, –	–	1.01, –	40.4, –	decrease
S, s	S Gulf St. Lawrence[7]	(Swain et al. 2009)	1959–2007	3–6	5.1, 1.1		0.71, 0.24	19.1, 7.1	decrease, increase
M	Gulf of Maine[8]	–	1970–1998	1–5	–	–	–	14.3	decrease
G	Georges Bank[8]	–	1970–1998	1–5	–	–	–	20.6	decrease
Haddock, *Melanogrammus aeglefinus*, Gadidae									
■	North Sea[4]	(ICES 2009a)	1974–2001	2–4	12.1	–	0.13	22.0	decrease
■, grey	W North Sea[9]	(ICES 2009a)	1976–2005	2	8.5	Regression	0.24	12.0	decrease
#	E North Sea[9]	(ICES 2009a)	1976–2005	2	–	Regression	–	–	–
□	Barents Sea[10]	(ICES 2009b)	1983–2003	4–6	2.9	Covariate	0.33	7.0	increase
Herring, *Clupea harengus*									
H	North Sea[11]	(ICES 2011)	1990–2006	2	2.9	–	0.26	5.15	decrease
American plaice, *Hippoglossoides platessoides*, Pleuronectidae									
▼, grey	2J3K[12]	–	1969–1999	4–9	–	–	–	15.6	decrease
European plaice, *Pleuronectes platessa*, Pleuronectidae									
▼	North Sea[13]	(ICES 2009a)	1955–1995	4	8.2	–	0.03	3.9	decrease

Common sole, *Solea solea*, Soleidae									
▲, Δ	North Sea [14]	(ICES 2009a)	1960–2002	2–4	10.9	Regression	0.05, 0.07	4.2, 17.1	decrease
Chum salmon, *Oncorhynchus keta*, Salmonidae									
C, c	Chitose River, Japan [15]	–	1973–1993	4	3.3, 2.1	–	0.21, 0.78	6.4, 23.9	decrease, increase
*, *	Nishibetsu River, Japan [15]	–	1973–1993	4	3.2, 2.0	–	0.17, 0.53	6.4, 23.9	decrease, increase
T, t	Tokachi River, Japan [15]	–	1973–1993	4	2.9, 1.8	–	0.09, 0.75	4.7, 26.5	decrease, increase

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References for traits: [1] M. Heino, unpublished data; [2] Pardoe et al. (2009); [3] Vainikka et al. (2009); [4] L. Marty, unpublished data, including maturity ogives; [5] Wright et al. (2011b); including maturity ogives; [6] L. Baulier, unpublished data; [7] Swain (2011); [8] Barot et al. (2004b); [9] Wright et al. (2011a), males only; [10] Devine and Heino (2011); [11] Enberg and Heino (2007); [12] Barot et al. (2005); [13] van Walraven et al. (2010); [14] Mollet et al. (2007), including maturity ogives; [15] Fukuwaka and Morita (2008).

Table 2. Results of regression through $\log_{10}$-transformed rates of mean and maximum phenotypic change (i.e., the rate numerator) in haldanes and darwins over time interval, including 95% confidence intervals (CI) of the slope.

Model	Slope	Intercept	n	95% CI (slope)
Haldanes				
Mean	0.09	-0.08	58	-0.15, 0.46
Maximum	0.07	0.02	58	-0.16, 0.42
Darwins				
Mean	0.62	4.58	64	0.31, 1.07
Maximum	0.70	4.45	64	0.36, 1,18

Table 3. Effect of total mortality and somatic growth on absolute rates of trait evolution in haldanes and darwins as fit by GAMMs.

Model	Effect of rate	F	N	p-value
Haldanes				
Mortality (Z, yr^{-1})	Positive	6.3	44	0.02
Growth (K, yr^{-1})	Negative	5.3	44	0.01
Darwins				
Mortality (Z, yr^{-1})	Negative	6.3	44	0.02
Growth (K, yr^{-1})	Not significant	–	–	–

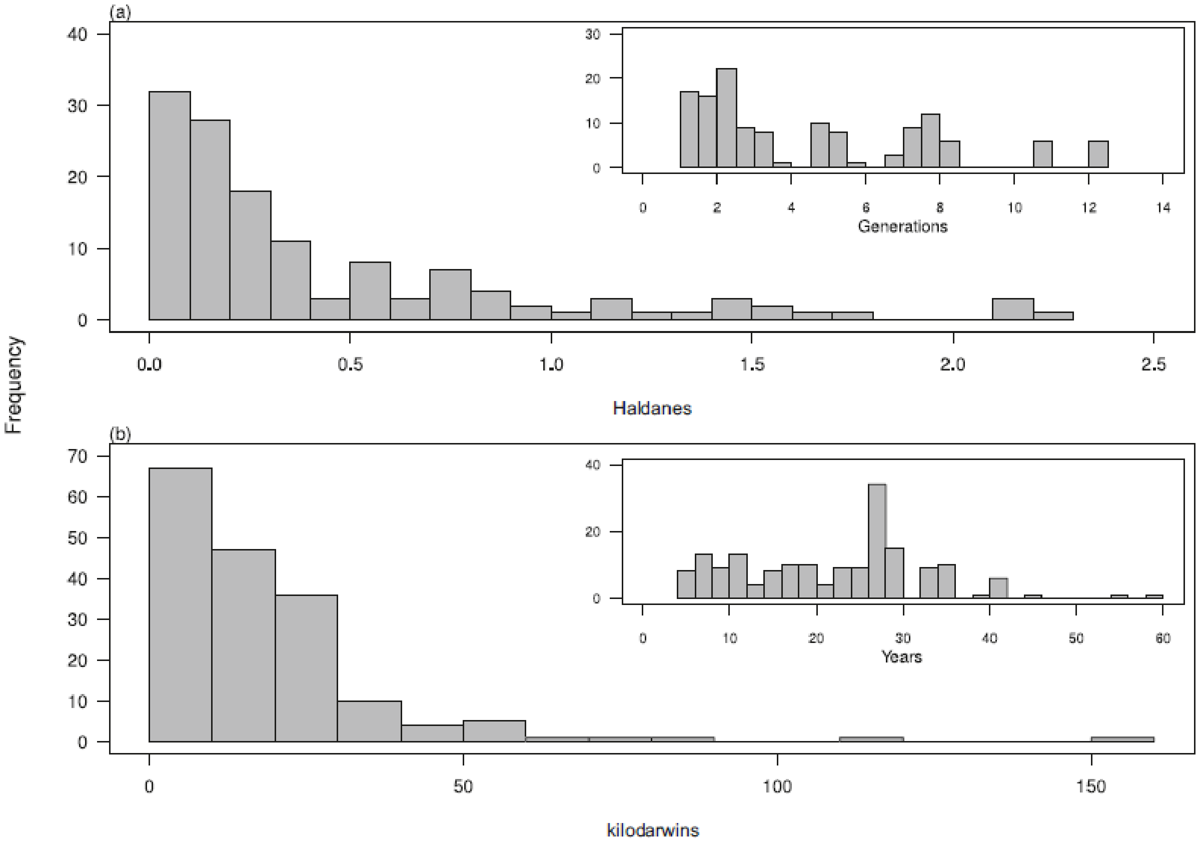

Figure 1. Histogram of absolute rates for haldanes (top) and Kdarwins (bottom) for life-history characteristics estimated from PMRN studies. Inserts are histograms of the number of generations (haldanes) and years (darwins).

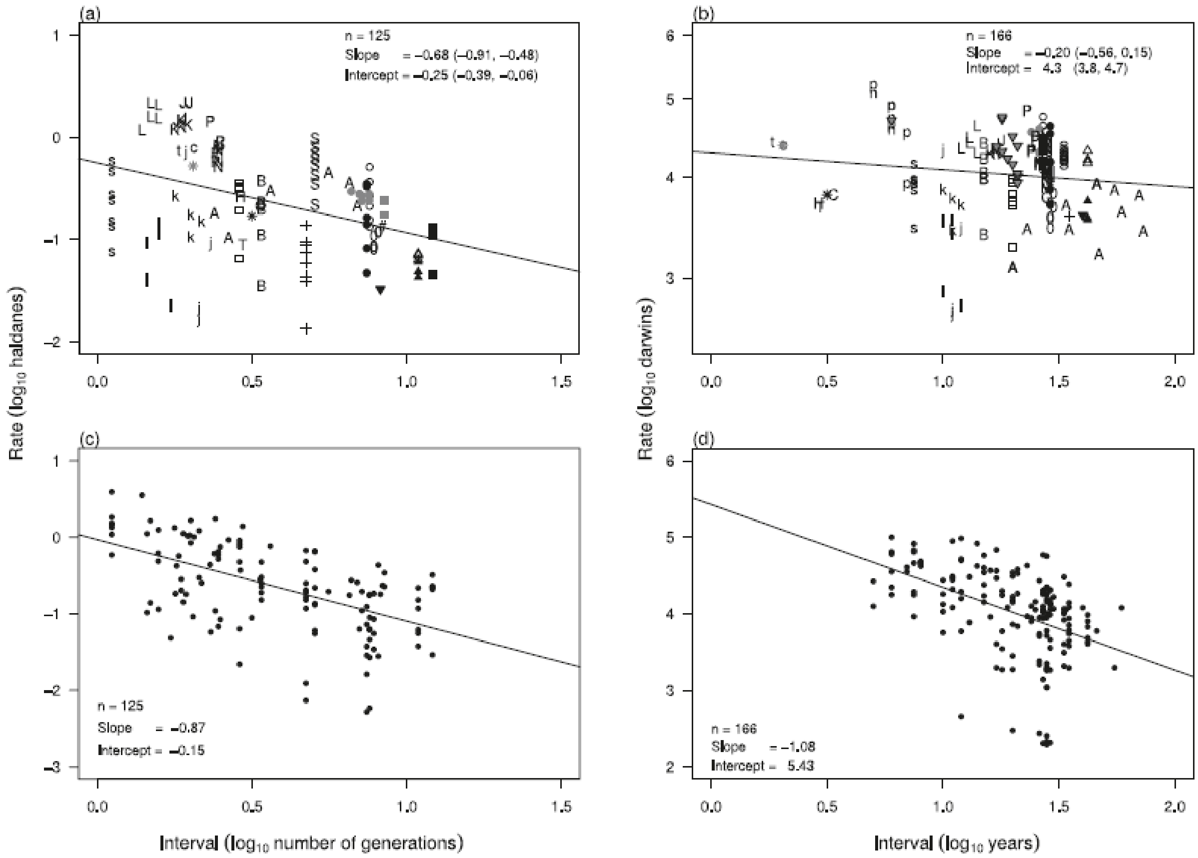

Figure 2. (top) Evolutionary rates in haldanes (left) and darwins (right) plotted as $\log_{10}$ rates over $\log_{10}$ time interval in number of generations (haldanes) or years (darwins). Each point represents a single rate for a stock-age-sex-trait combination; symbol definition is in Table 1. Because rates tend to scale negatively with time, a trend line, estimated from a linear mixed effects model where stock + period was included as a random effect, is shown so that rates faster or slower than the mean predicted value can be evaluated. (bottom) Randomized log-rate versus log-interval (LRI) plot for haldanes (left) and darwins (right), where numerators were randomized with respect to the number of generations or years (see Kinnison and Hendry 2001). All rates were expressed as absolute values as the direction of change was not relevant in comparing the relative speed of trait change between stocks. Cod stocks 3NO and 3Ps, where the number of generations was < 1, were not included in the haldane plots.

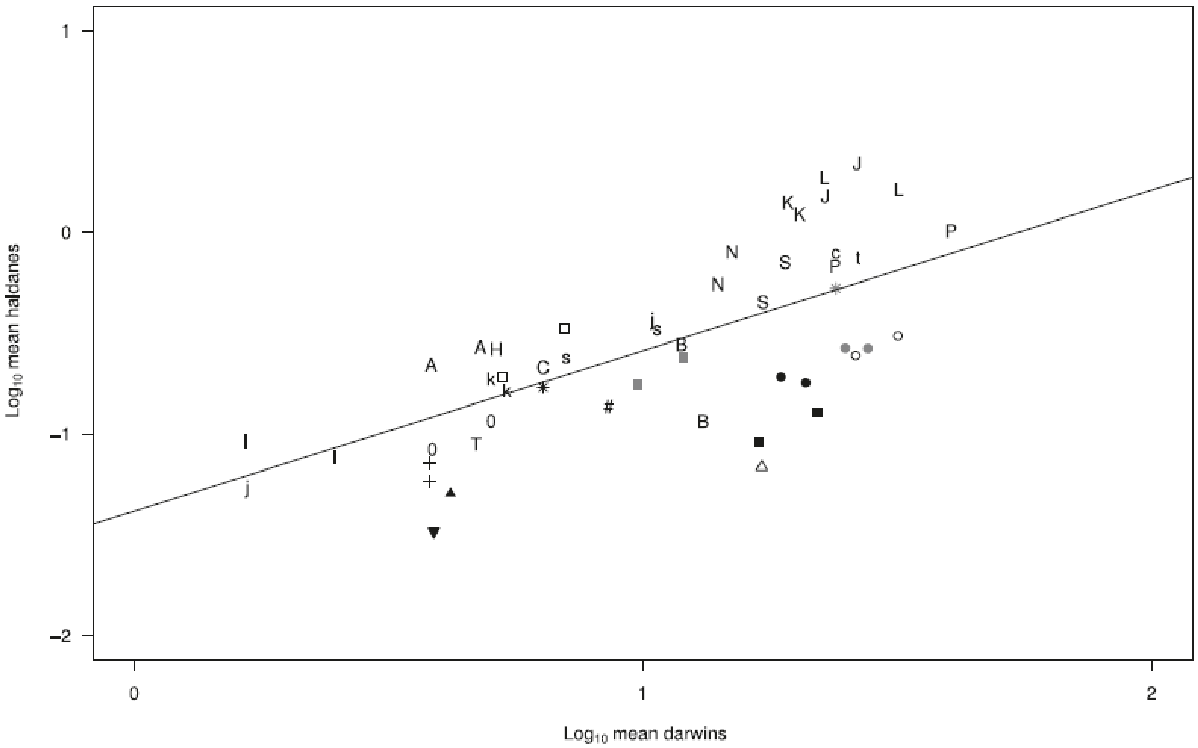

Figure 3. Comparison of estimated rates of evolution specified in $\log_{10}$ haldanes against $\log_{10}$ darwins. Each point represents an average absolute rate, where rates for both sexes are shown. Symbols are defined in Table 1. Linear mixed effects regression line is shown.

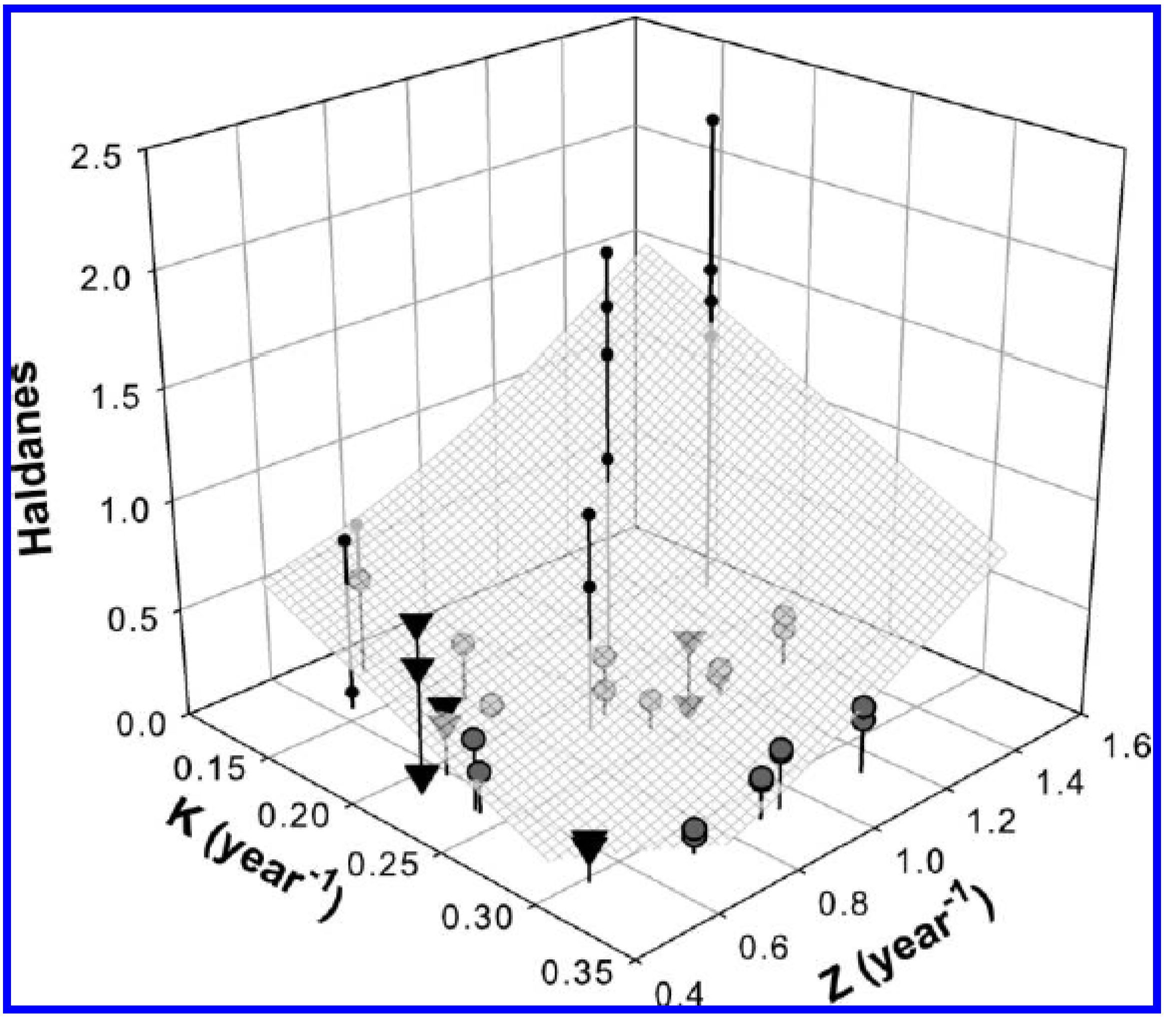

Figure 4. Response shape of the GAMM relationship between rates of evolution in haldanes, total mortality (Z, yr^{-1}), and somatic growth (K, yr^{-1}) for gadoid stocks. Black circles are post-moratorium, grey circles include pre- and no moratorium stocks.

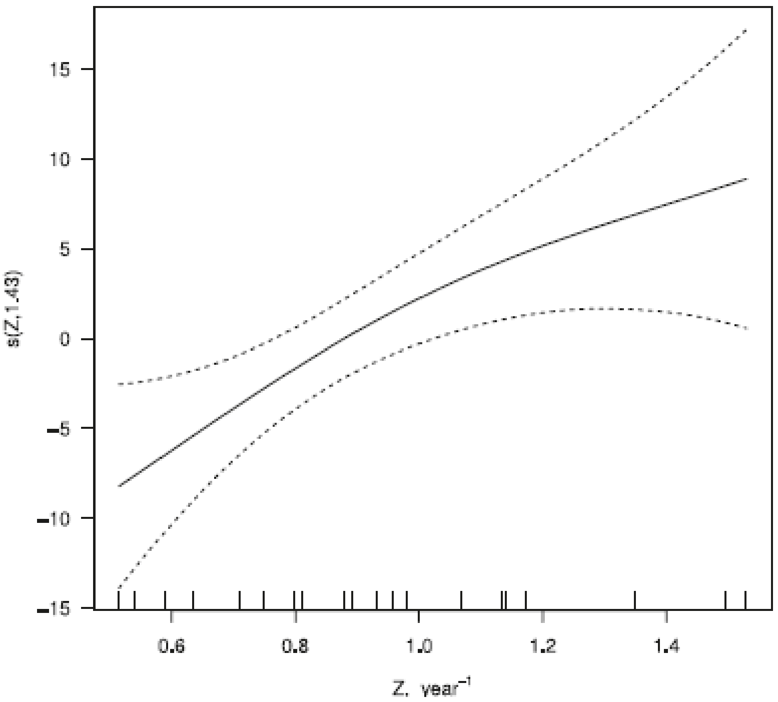

Figure 5. Response shape of total mortality, Z (yr^{-1}), in the final GAMM model for rates in darwins for gadoid stocks. The dashed lines are the 95% pointwise confidence intervals, tick marks show the location of observations along the variable range, the y-axis represents the effects of the respective variables, and *s* is a smoother term of the GAMM.