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Fisheries-induced rates of contemporary evolution: Comparing Haldanes and Darwins

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Trait evolution over time periods spanning generations, not millennium, 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 length (or weight) at maturation from probabilistic maturation reaction norm midpoints for fish stocks from the Northwest Atlantic, Northeast Arctic and Barents Sea, and the North Sea. For stocks that had a moratorium enacting during the time period, rates were estimated for pre- and post-moratorium. Absolute rates in haldanes for 17 stocks ranged from 0.02–1.9 and from 0.5–153 in kdarwins (10^3 darwins) for 21 stocks. The North Sea and northwest Atlantic (pre-moratorium) cod stocks had some of the fastest rates of change (in haldanes), while post-moratorium northwest Atlantic and Icelandic cod stocks had the slowest rates. North sea sole and plaice haldane rates also tended to be slower than the average rate. When comparing rates in darwins, all stocks in the North Sea and Grand Banks, and cod stocks in the Gulf of Maine and 2J3KLNOPs (pre-moratorium time series) experienced some of the fastest evolutionary rates of change. Stating whether fisheries-induced evolution is fast or slow has limited ecological meaning, and the focus should now be towards determining whether the rate of fisheries-induced evolution is fast enough to permanently alter ecosystem dynamics. The next stage should be to investigate the effect of these relatively fast rates of phenotypic change in terms of fisheries yields and sustainability.

Keywords: haldanes, darwins, contemporary evolution, rates of change

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INTRODUCTION

Rapid or contemporary evolution, i.e., trait evolution in less than a few hundred generations, (Hendry and Kinnison, 1999), is increasingly observed in natural populations. Human-induced phenotypic changes have been shown to be above the natural baseline for evolution (Hendry et al., 2008; Darimont et al., 2009). In exploited fish stocks, there are many examples of phenotypic changes occurring within a few generations that have been interpreted as human-induced evolution (e.g., Law, 2000; Sharpe and Hendry, 2009; Jørgensen et al., 2007; Olsen et al., 2004). However, there is some debate over whether the observed rates of phenotypic/genotypic change should be considered fast or slow – some have argued rates are fast (Jørgensen et al., 2007), while others have argued that the expected theoretical change is at a more modest rate (Andersen and Brander, 2009).

Evolutionary change has typically been quantified in darwins (Haldane, 1949), although it is increasingly reported in haldanes (Gingerich, 1993). The darwin represents the relative rate of change on an absolute time scale, and tends to be used because of the ease of its estimation and for comparison to previous studies. But the darwin was not designed for quantifying rates of contemporary evolution; its intended application was long temporal scales, i.e., to traits from the fossil record (Hendry and Kinnison, 1999). The darwin is useful primarily for ratio scale data because it represents proportional changes in units of e per million years (Kinnison and Hendry, 2001). The haldane was proposed to estimate the change in a population trait in units of standard deviation per generation (Gingerich, 1993). 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 (Hendry and Kinnison, 1999). The haldane has the advantage of being applicable to ratio and interval scale data, is on the time scale over which evolution takes place, and is more widely comparable than the darwin (Hendry and Kinnison, 1999; Gingerich, 2001; Gingerich, 1993). However, it 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. Haldanes and darwins, although correlated, are not the same, and comparisons of the two should provide insight into common evolutionary patterns (Gingerich, 2001).

Evolutionary rates are not independent of the time interval over which they are measured. Because rates of phenotypic change decline with increasing time intervals (partially as an artifact of the negative self-correlation caused by plotting rates), rates must be interpreted

relative to the time interval over which they were measured, or as deviations from the average trend over time (Gingerich, 2001; Stockwell et al., 2003). One method is to analyse the absolute amount of phenotypic change over time (Hendry et al., 2008), which is simply the amount of change divided by the phenotypic standard deviation or, for darwins, the amount of change. Another is the log-rate versus log-interval (LRI) method of Gingerich (1993), which estimates the mean absolute rate of evolutionary change over one generation. The LRI method can be used over short temporal scales to compare rates of change among species, but it has limited applicability over longer time intervals (Hendry and Kinnison, 1999).

Here we attempt to define the relative speed of trait change by estimating contemporary rates of evolution in haldanes and darwins for length (or weight) at maturation from probabilistic maturation reaction norm midpoints (Heino et al., 2002a) for several fish stocks from the Northwest Atlantic, Northeast Arctic and Barents Sea, and the North Sea. Some of these stocks currently support fisheries, while others have been under moratorium for several decades. Several of the original analyses have accounted for environmental factors in the reaction norm estimation (Table 1).

METHODS

Haldanes, the rate of change in standard deviations per generation, were estimated using the procedure outlined by Gringerich (1993) and Hendry & Kinnison (1999) as the change in the trait over the time period (estimated from linear regression on the log-transformed trait over time), divided by the product of the phenotypic standard deviation and the number of generations spanning the time period. To estimate phenotypic standard deviation where only the width of the reaction norm (length interval over which maturation probability increases from 25% to 75%) was known (typically when traits were estimated using the demographic PMRN method; Barot et al., 2004a), the slope parameter was estimated from the relationship corresponding to the logistic curve, multiplied by a correction factor of $\pi/\sqrt{3}$. Otherwise, the phenotypic standard deviation was simply the product of inverse of the slope multiplied by the correction factor stated above. Life-history traits, primarily length-at-maturation, were chosen from studies where data on reaction norm width (demographic method) or slope (direct method) were readily available, either from the authors directly or from the literature (Table 1).

Generation time for a particular stock was approximated using the method of Froese and Binohlan (2000) as

$$t_g \approx t_{opt} = \frac{\sum_{t_m}^{t_{max}} t * S_t * W_t}{\sum_{t_m}^{t_{max}} S_t * W_t},$$

where t_g is generation time, t_{opt} is age of maximum egg production, S_t is number of survivors to age t , and W_t is the average weight at age t . S_t can be set equal to the estimated numbers of reproductive individuals at age. Data for maturity ogives for most stocks (unless otherwise indicated in Table 1), numbers- and weights-at-age were from gathered stock assessment reports.

Darwins were estimated as $d = \frac{\ln(Z_1/Z_0)}{\Delta t \times 10^{-6}}$, where Z_0 and Z_1 were values estimated for the beginning and end of the time series from linear regression on log-transformed traits over time, and $\Delta t = t_1 - t_0$ (Haldane, 1949). A change of one darwin means that the trait would increase by a factor e in one million years.

If the series included a moratorium or a period of large change in fishing intensity, rates were estimated for the entire period and for pre- and post-moratorium periods. This was done because time series should be examined for shifts in trait evolution when selective pressures significantly change (Hendry and Kinnison, 1999).

Generational rates, representing the mean absolute rate of evolutionary change over one generation were estimated using the log-rate versus log-interval (LRI) method of Gingerich (1993). Rates estimated over different intervals are not directly comparable, hence the use of the \log_{10} scale. The LRI method aids in defining the magnitude of trait change, and is one way to test for directional change, random change, or stasis. To interpret rates relative to the time interval over which they were measured, the effects of time interval on mean phenotypic change was also analyzed. Phenotypic change was averaged for all ages within a stock and was used as an estimate of the amount of change that might be accomplished (Kinnison and Hendry, 2001). Absolute values were used because the direction of change was not relevant in comparing the relative speed between stocks. Regression parameters were bootstrapped to obtain 95% confidence intervals.

RESULTS

The number of generations for the time period of study for all stocks ranged from 2-11, but when pre- and post-moratorium periods were considered, the number of generations for two

stocks (Atlantic cod 3NO and 3Ps) was less than one (Table 1). Haldane rates estimated for less than one generation could be considered too uncertain, therefore those two stocks were omitted from the haldane-only analyses.

Median absolute evolutionary rates in haldanes for 17 stocks and in kdarwins (10^3 darwins) for 21 stocks were 0.455 and 12.97, respectively (Tables 2, 3). Generally, the North Sea and northwest Atlantic (pre-moratorium) cod stocks had some of the fastest rates of change (haldanes), while Icelandic and post-moratorium northwest Atlantic cod stocks had the slowest rates. North Sea sole and plaice haldane rates also tended to be slower than the average rate (Figure 1). When comparing rates in darwins, all stocks in the North Sea and Grand Banks, as well as the Gulf of Maine and 2J3KLNOPs (pre-moratorium time series) cod stocks experienced some of the fastest evolutionary rates of change. Northeast Arctic cod, Icelandic cod, North Sea sole and plaice, and Barents Sea haddock had accounted for environmental factors in their reaction norm estimation and were generally slower than the average rate of change.

Generational rates in haldanes and darwins were negatively correlated with the length of time over which they were measured (Figure 1). The slope was less pronounced for both types of rates when Northwest Atlantic cod (stocks 2J3KL) post-moratorium rates were added. The bootstrapped (bias corrected) confidence interval of the slope for haldanes was wide (-1.02, -0.24). Although the confidence interval approached the value of 0, typifying directional change, it did include -0.5, indicative of random change, and -1, which is indicative of stasis (Gingerich, 1993). The predicted generational rate (h_0) of the haldane was 0.71, with confidence intervals ranging from 0.39 to 1.19. The LRI relationship for darwins is not discussed further.

Neither slopes of the regression of phenotypic change in haldanes or darwins were significantly different from 0 (haldanes: $p = 0.39$, 95% CI = -0.14, 0.85; darwins: $p = 0.17$, 95% CI = -0.002, 0.01, Figure 2). The general trend for both relationships was a slight increase. Insignificant relationships between phenotypic change and time interval generally signify that, although the amount of change may be large, the distribution of the observed changes is similar at long and short temporal scales (Hendry et al., 2008).

Rates in haldanes and darwins showed a high degree of correlation (Figure 3). For most species included in this study, low rates in haldanes were coupled with lower rates in darwins or vice versa. Northeast Arctic cod, North Sea cod, and North Sea haddock showed a larger spread of rates in darwins for relatively little rate change in haldanes.

DISCUSSION

Evolutionary rates and phenotypic changes of length at maturation estimated from reaction norms for several fish stocks were similar to rates of change in perturbed species published elsewhere (Hendry et al., 2008; Kinnison and Hendry, 2001; Gingerich, 1993). Hendry et al. (2008) show phenotypic changes as a result of anthropogenic change are as high as 8 standard deviation units (haldanes) while we have estimated changes as high as 10 standard deviation units, although most are typically less than 4. As such, our results support earlier evidence that phenotypic change for species associated with anthropogenic disturbance is typically faster than for those under only natural selection, and much faster than in wild populations (Hendry et al., 2008; Darimont et al., 2009). The amount of phenotypic change for haldanes was independent of the time interval, which is consistent with what has been reported elsewhere, where phenotypic changes were shown either to be independent of the time interval or to increase with increasing time (Hendry et al., 2008; Kinnison and Hendry, 2001). Changes in units of e (darwins) were generally faster than those published in a meta-analysis by Hendry et al. (2008). These differences may be partially explained by the shorter time interval over which we estimated change – maximum time interval 44 years as opposed to 150 years. Macroevolution, evolution over hundreds or more generations, tends to be slower than microevolution (evolution from 2-100s of generations; Gingerich, 1993), and evolutionary change slows with increasing time after the disturbance (Hendry et al., 2008; Kinnison and Hendry, 2001; Reznick et al., 1997). Short timescales tend to capture dramatic changes, where the initial response to the perturbation is large (Stockwell et al., 2003), which then slows with increasing time from the disturbance.

Gingerich (2001) has shown that slopes approaching -1.0 from the log-rate log-interval analysis are consistent with stasis, or stabilizing processes, while slopes around -0.5 are indicative of randomness, but notes that processes can interact to produce results that are indistinguishable from randomness. The 95% confidence intervals of the slope generated here included both -0.5 and -1, and it seems contradictory to use the LRI-scale to state evolution in these stocks was slow or random (i.e., a neutral mixture of directional and stabilizing selection) when our rates are similar to ‘fast’ rates published elsewhere (Hendry et al., 2008; Darimont et al., 2009). Stasis can refer to a pattern of multiple reversals, or high variability, in short-term rates, such that there is no net change over long intervals (Gingerich, 2001; Kinnison and Hendry, 2001; Gingerich, 1993). The time scale over which our study focused has generally been relatively short, so this may not be a plausible explanation. Rates for all of

the stocks were analyzed over fewer than 10 generations, and over half of the original analyses were over less than 5 generations. Variation and reversals in evolutionary trajectories is common in many contemporary evolution and paleontological studies, and can be highly dependent on the choice of years included in the linear rate estimation (Hendry and Kinnison, 1999).

Uncertainty in darwin or haldane estimates can result from errors in the estimation of the amount of elapsed time (years or generations), whereas 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. Inaccurate estimates of elapsed time are the most serious. Generation time is expected to change as age- and size-at-maturation change, and ideally, one should use pre-exploitation estimates, if available. One could argue that changes in generation time in conjunction with the estimated changes in age at maturation should be allowed and accounted for in haldane estimations. Using only pre-exploitation generation time estimates was not done here and will be included in the next stage as part of the sensitivity analysis. If the total time interval of trait change is short, errors can be much larger than expected and 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.

The comparison of rates in haldanes and darwins showed a high degree of correlation. This is expected and is because the rates for both are expressed as a phenotypic difference per unit of time (Hendry and Kinnison, 1999). A few stocks showed a spread of darwin rates over relatively consistent haldane rates. Differences in rates such as those shown, or high-low/low-high combinations, can be caused by variation in the estimated generation time for a given age class.

Generational rate of change in haldanes for stocks presented here was 0.7 standard deviations per generation on a time scale of one generation, i.e., the average difference between successive generations. This rate is much higher than that reported by Gingerich (1993), who found that intrinsic rates of haldane change tended to be low and in the order of approximately 0.1 standard deviations per generation. Generational rate of change of these 17 stocks was similar to a meta-analysis of 2151 rates by Kinnison and Hendry (2001), indicating that the rate reported by Gingerich (1993) may be much lower than that typically seen in populations experiencing human-induced changes. Studies analyzing multiple populations have often shown estimated rates that are faster or slow than the mean predicted rate

(Gingerich, 1993; Hendry et al., 2008; Hendry and Kinnison, 1999; Gingerich, 2001; Kinnison and Hendry, 2001). Whether this rapidity is rare or often encountered in nature (but not reported) has been questioned by Hairston et al. (2005).

Our analysis suggests that the rates of fisheries-induced evolution are comparable to other examples of human-induced evolution. Fast rates of change should be expected as this means the population can respond to changing selection pressures quickly and hence avoid extinction. However, Hairston et al. (2005) argue that the speed of evolutionary rates only matters in an ecological context if they are fast enough to alter the outcomes of ecological interactions. Stating whether fisheries-induced evolution is fast or slow has no ecological meaning, and the focus should now be towards determining whether the rate of fisheries-induced evolution is fast enough to permanently alter ecosystem dynamics. The next stage will be to use this information as a descriptor of good (or poor) environmental status by determining the importance of these rates of change in phenotypic traits to yield and fishing sustainability.

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Table 1. Time period of study and number of generations for each stock, including pre- and post-moratorium periods, and whether environment was included as an explanatory variable in the original analysis. Stocks missing the number of generations were used only in the estimation of darwins due to lack of data phenotypic variation. Symbols refer to those plotted in Figure 3; filled and unfilled symbols refer to pre- and post-moratorium periods for cod, and Lp₅₀ and Wp₅₀ for North Sea plaice.

Symbol	Stock	Time period	No. Generations	Pre	Post	Environment
A	NE Arctic cod ¹	1932–2008	2.66–8.56			Yes
I	Icelandic cod ²	1968–2007	4.73			Yes
B	Baltic cod ³	1987–2003	3.39			
○	North Sea cod ⁴	1963–1999	5.99			
●	North Sea cod ⁵ (southern)	1976–2005	7.33			
●	North Sea cod ⁵ (northwest)	1976–2005	6.96			
△, ▲	North Sea sole ⁶	1962–2006	10.90			Yes
■	North Sea haddock ⁴	1963–2008	8.12			
■, grey fill	North Sea haddock ⁵ (west)	1976–2005	8.49			
■, grey fill	North Sea haddock ⁵ (east)	1976–2005	8.37			
●	North Sea plaice ⁷	1957–2006	8.24			Yes
■, □	2J cod ⁸	1973–2005	3.93–4.14	1.98–2.15	1.93–2.33	
▲, △	3K cod ⁸	1973–2005	3.79–3.98	1.94–2.12	1.79–2.17	
◆, ◇	3L cod ⁸	1967–2005	3.45–3.66	1.54–1.72	1.45–1.73	
*	3NO cod ⁸	1967–2005	3.25	2.57	<1	
+	3Ps cod ⁸	1967–2007	3.10–3.42	2.44–2.63	<1	
□	Barents Sea haddock ¹⁰	1983–2003	2.88			Yes
	Gulf of Maine cod ¹¹					
	Grand Banks cod ¹²					
	<i>Coregonus</i> ¹³					
	Lake Constance					
	2J3K Am. plaice ¹⁴					

References for traits: ¹ M. Heino, pers. comm.; ² Pardoe et al. (2009); ³ Vainikka et al. (2009); ⁴ L. Marty, unpublished data, incl. maturity ogives; ⁵ Wright et al. (2010), incl. maturity ogives; ⁶ F. Mollet, pers. comm., incl. maturity ogives; ⁷ van Walraven et al. (2010); ⁸ L. Baulier, unpublished manuscript; ⁹ Devine, unpub. data; ¹⁰ Barot et al. (2004b); ¹¹ Thomas et al. (2009); ¹² Bowering et al. (1997).

Table 2. Haldane rates by stock, sex, and age-class for maturation reaction norms in length- (L_{p50}) and weight-at-maturation (W_{p50}). The time period post-moratorium for Atlantic cod stocks 3NO and 3Ps was less than one generation and haldanes were not estimated. *Italicized numbers indicate the time period was between 1–2 generations. Time period for NE Arctic cod varied, see Heino et al. (2002b).*

Stock	Trait	Sex	Time	Age									
				2	3	4	5	6	7	8	9	10	
NE Arctic cod*	Lp50	Both	Varies				-0.105	-0.455	-0.334	-0.147	-0.106	0.175	
NE Arctic cod*	Lp50	Both	Varies				-0.105	-0.455	-0.361	-0.215	-0.301	0.182	
Icelandic cod	Lp50	Male	1964–1999			-0.087	-0.074	-0.044	-0.059	-0.094			
Icelandic cod	Lp50	Female	1964–1999			0.043	-0.013	-0.039	-0.059	-0.136			
Baltic cod	Lp50	Female	1988–2003	-0.232	-0.225	-0.377							
Baltic cod	Lp50	Male	1988–2003	0.036	-0.111	-0.200							
North Sea sole	Lp50	Both	1960–2002	0.049	0.043	0.060							
North Sea sole	Wp50	Both	1960–2002	0.070	0.063	0.072							
North Sea haddock	Lp50	Female	1974–2001	-0.133	-0.120	-0.131							
North Sea haddock	Lp50	Male	1974–2001	-0.109	-0.119	-0.045							
North Sea cod	Lp50	Female	1974–2001	-0.155	-0.213	-0.367							
North Sea cod	Lp50	Male	1974–2001	-0.133	-0.268	-0.515							
North Sea plaice	Lp50	Female	1955–1995			-0.033							
North Sea cod (northwest)	Lp50	Female	1976-2005		-1.137								
North Sea cod (northwest)	Lp50	Male	1976-2005		-1.222								
North Sea cod (south)	Lp50	Female	1976-2005		-1.184								
North Sea cod (south)	Lp50	Male	1976-2005		-1.284								
North Sea haddock (west)	Lp50	Female	1976-2005	-0.773									
North Sea haddock (west)	Lp50	Male	1976-2005	-0.876									
North Sea haddock (east)	Lp50	Male	1976-2005	-0.585									
Barents Sea haddock	Lp50	Female	1983-2003			0.604	0.820	1.264					
Barents Sea haddock	Lp50	Male	1983-2003			0.318	0.192	0.065					

Table 2 continued.

Stock	Time	Moratorium	Sex	Age			
				4	5	6	7
Atlantic cod							
2J	1977–2007		Female	-0.688	-0.961		
2J	1977–1992	Pre	Female	-1.989	-1.885		
2J	1992–2007	Post	Female	-0.021	<i>0.703</i>		
3K	1977–2007		Female	-0.613	-0.499		
3K	1977–1992	Pre	Female	-1.396	-1.232		
3K	1992–2007	Post	Female	-0.106	-0.268		
3L	1981–83, 1985–2007		Female	-0.592	-0.437		
3L	1981–83, 1985–1992	Pre	Female	-1.898	-1.378		
3L	1992–2007	Post	Female	-0.144	-0.040		
3Lspr*	1981–83, 1985–2007		Female	-0.653	-1.032		
3Lspr*	1981–83, 1985–1992	Pre	Female	-1.160	-1.754		
3Lspr*	1992–2007	Post	Female	<i>0.705</i>	<i>0.861</i>		
3NO	1971–1982, 1984–2005,2007		Female	-0.680	-0.624		
3NO	1971–1982, 1984–1994	Pre	Female	-0.788	-0.679		
3NO	1994–2005, 2007	Post	Female	–	–		
3Ps	1972–1973, 1975–2005,2007		Female	-0.485	-0.570	-0.402	
3Ps	1972–1973, 1975–1993	Pre	Female	-0.663	-0.820	-0.813	
3Ps	1993–2005, 2007	Post	Female	–	–	–	
2J	1977–2007		Male	-0.617	-0.646		
2J	1977–1992	Pre	Male	-1.359	-1.438		
2J	1992–2007.	Post	Male	-0.090	-0.016		
3K	1977–2007		Male	-0.544	-0.400		
3K	1977–1992	Pre	Male	-1.026	-1.021		
3K	1992–2007.	Post	Male	-0.151	-0.176		
3L	1981–83, 1985–2007		Male	-0.392	-0.447	-0.531	
3L	1981–83, 1985–1992	Pre	Male	-1.103	-1.313	-1.733	
3L	1992–2007	Post	Male	-0.023	-0.114	0.093	
3Lspr*	1981–83, 1985–2007		Male	-0.457	-0.559		
3Lspr*	1981–83, 1985–1992	Pre	Male	-0.817	-1.008		
3Lspr*	1992–2007	Post	Male	<i>0.550</i>	<i>0.612</i>		
3NO	1971–1982, 1984–2005,2007		Male	-0.607	-0.582		
3NO	1971–1982, 1984–1994	Pre	Male	-0.588	-0.503		
3NO	1994–2005, 2007	Post	Male	–	–		
3Ps	1972–1973, 1975–2005,2007		Male	-0.500	-0.755		
3Ps	1972–1973, 1975–1993	Pre	Male	-0.553	-0.719		
3Ps	1993–2005, 2007	Post	Male	–	–		

* 3Lspr refers to stock 3L, where data were collected during spring surveys. All other estimates were based on data from autumn surveys.

Table 3. Rates in kdarwins by stock, sex, and age-class for maturation reaction norms in length- (L_{p50}) and weight-at-maturation (W_{p50}). The time period post-moratorium for Atlantic cod stocks 3NO and 3Ps was less than one generation and haldanes were not estimated. Time period for NE Arctic cod varied, see Heino et al. (2002b).

Stock	Trait	Sex	Time	Average	Age										
					1	2	3	4	5	6	7	8	9	10	
NE Arctic cod*	Lp50	Both	Varies	3.8						1.2	8.4	6.3	2.7	1.6	2.8
NE Arctic cod*	Lp50	Both	Varies	4.8						1.2	8.4	7.2	4.2	4.9	2.8
Icelandic cod	Lp50	Both	1964–1999	3.8											
Baltic cod	Lp50	Female	1988–2003	11.9		9.6	9.6	16.5							
Baltic cod	Lp50	Male	1988–2003	13.1		2.5	11.3	25.6							
North Sea sole	Lp50	Both	1960–2002	4.2		3.5	3.6	5.5							
North Sea sole	Wp50	Both	1960–2002	17.1		14.8	16.0	20.6							
North Sea haddock	Lp50	Female	1974–2001	16.9		15.8	20.7	29.5							
North Sea haddock	Lp50	Male	1974–2001	22.0		15.0	22.4	13.4							
North Sea cod	Lp50	Female	1974–2001	26.2		13.6	22.1	43.0							
North Sea cod	Lp50	Male	1974–2001	31.7		12.2	26.2	56.8							
North Sea plaice	Lp50	Female	1955–1995	3.9				3.9							
North Sea cod (northwest)	Lp50	Female	1976-2005	20.7			20.7								
North Sea cod (northwest)	Lp50	Male	1976-2005	27.5			27.5								
North Sea cod (south)	Lp50	Female	1976-2005	21.2			21.2								
North Sea cod (south)	Lp50	Male	1976-2005	11.7			11.7								
North Sea haddock (west)	Lp50	Female	1976-2005	10.0		10.0									
North Sea haddock (west)	Lp50	Male	1976-2005	11.0		11.0									
North Sea haddock (east)	Lp50	Male	1976-2005	9.3		9.3									
Barents Sea haddock	Lp50	Female	1983-2003	7.0				5.0	6.5	9.5					
Barents Sea haddock	Lp50	Male	1983-2003	5.3				8.7	5.3	1.9					

Table 3 continued.

Stock	Trait	Sex	Time	Average	Age									
					1	2	3	4	5	6	7	8	9	10
American plaice 2J3K	Lp50	Female	1969–1999	15.6				8.6	11.0	14.1	16.6	20.1	23.2	
American plaice 2J3K	Lp50	Male	1969–1999	37.4				31.1	23.7	52.6	56.2	50.8	10.1	
<i>Coregonus lavaretus</i> Lake Constance	Fecundity	Female	1963–1999	5.8										
Georges Bank cod	Lp50	Female	1970-1998 (cohorts)	20.6	8.6	12.9	18	35	28.7					
Georges Bank cod	Lp50	Male	1970-1998 (cohorts)	11.7	6	10.8	12	12.4	17.4					
Gulf of Maine cod	Lp50	Female	1970-1998 (cohorts)	14.3	12.8	9.8	11.6	12	25.1					
Gulf of Maine cod	Lp50	Male	1970-1998 (cohorts)	19.5	25.2	21	13.2	7.6	30.5					

Table 3 continued.

Stock	Time	Moratorium	Sex	Age			
				4	5	6	7
Atlantic cod							
2J	1977–2007		Female		10.6	16.4	
2J	1977–1992	Pre	Female		23.5	24.7	
2J	1992–2007	Post	Female		0.5	20.4	
3K	1977–2007		Female		10.6	9.0	
3K	1977–1992	Pre	Female		19.1	18.1	
3K	1992–2007	Post	Female		2.8	7.3	
3L	1981–83, 1985–2007		Female		9.6	7.4	
3L	1981–83, 1985–1992	Pre	Female		23.2	17.8	
3L	1992–2007	Post	Female		2.5	0.8	
3Lspr*	1981–83, 1985–2007		Female		13.4	21.7	
3Lspr*	1981–83, 1985–1992	Pre	Female		18.3	27.3	
3Lspr*	1992–2007	Post	Female		18.3	27.1	
3NO	1971–1982, 1984–2005,2007		Female		13.0	13.1	
3NO	1971–1982, 1984–1994	Pre	Female		14.3	13.5	
3NO	1994–2005, 2007	Post	Female		–	–	
3Ps	1972–1973, 1975–2005,2007		Female		17.0	22.8	40.9
3Ps	1972–1973, 1975–1993	Pre	Female		20.4	29	59.3
3Ps	1993–2005, 2007	Post	Female		–	–	–
2J	1977–2007		Male	12.4	13.7		
2J	1977–1992	Pre	Male	20.9	23.5		
2J	1992–2007.	Post	Male	2.8	0.5		
3K	1977–2007		Male	11.8	8.9		
3K	1977–1992	Pre	Male	16.9	18.1		
3K	1992–2007.	Post	Male	5	5.8		
3L	1981–83, 1985–2007		Male	9.9	12.0	15.5	
3L	1981–83, 1985–1992	Pre	Male	21.5	26.2	36.3	
3L	1992–2007	Post	Male	0.6	3.5	3.4	
3Lspr*	1981–83, 1985–2007		Male		11.2	15.2	
3Lspr*	1981–83, 1985–1992	Pre	Male		15.2	20.7	
3Lspr*	1992–2007	Post	Male		18.1	25	
3NO	1971–1982, 1984–2005,2007		Male		15.6	17.3	
3NO	1971–1982, 1984–1994	Pre	Male		14.2	13.8	
3NO	1994–2005, 2007	Post	Male		–	–	
3Ps	1972–1973, 1975–2005,2007		Male		19.1	32.3	
3Ps	1972–1973, 1975–1993	Pre	Male		19.3	26.4	
3Ps	1993–2005, 2007	Post	Male		–	–	

* 3Lspr refers to stock 3L, where data were collected during spring surveys. All other estimates were based on data from autumn surveys.

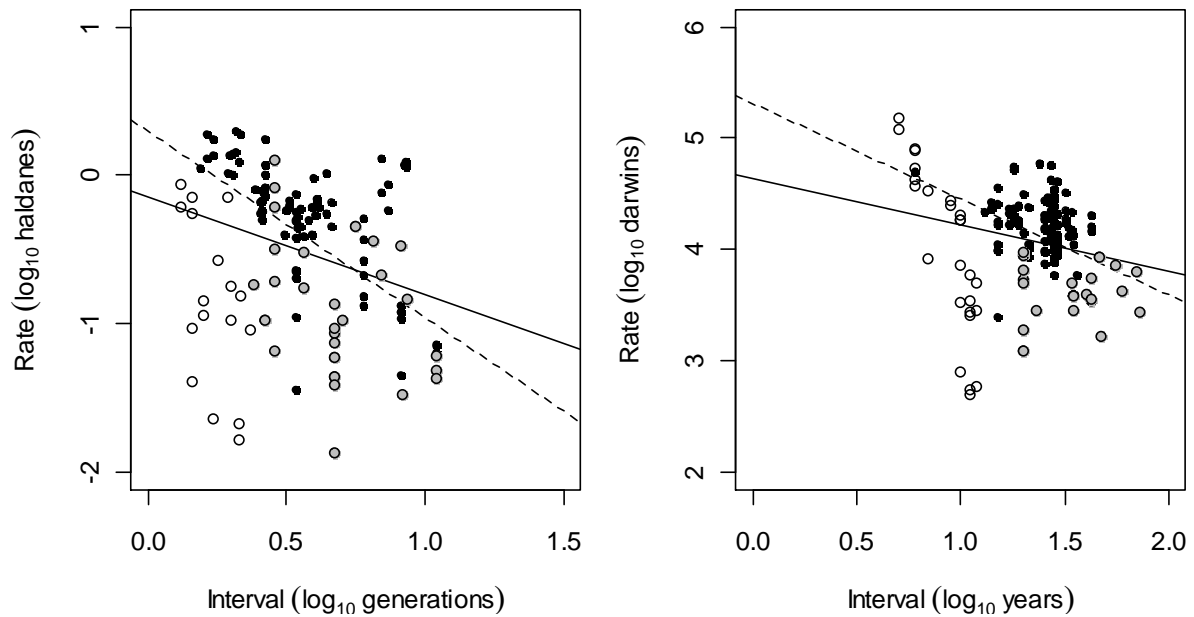


Figure 1. Distribution of evolutionary rates in haldanes and darwins for the stocks in this study, expressed as \log_{10} rates over \log_{10} time interval in generations or years. All rates were expressed as absolute values. Each point represents a single rate for a stock-age-sex combination; grey points are those data that accounted for environmental factors in the PMRN estimation. Because rates tend to scale negatively with time, a trend line is shown so that rates faster or slower than the mean predicted value can be evaluated. Open circles are Northwest Atlantic cod stocks post-moratorium rates; stocks where the number of generations for the measured trait was <1 were not include in the haldane plot. Solid line is the trend in rate change using all shown data (haldanes: slope = -0.66 , intercept = -0.15 ; darwins: slope = -0.42 , intercept = 4.64), and dashed line is the trend excluding post-moratorium rates (haldanes: slope = -0.661 , intercept = 0.29 ; darwins: slope = -0.86 , intercept = 5.31).

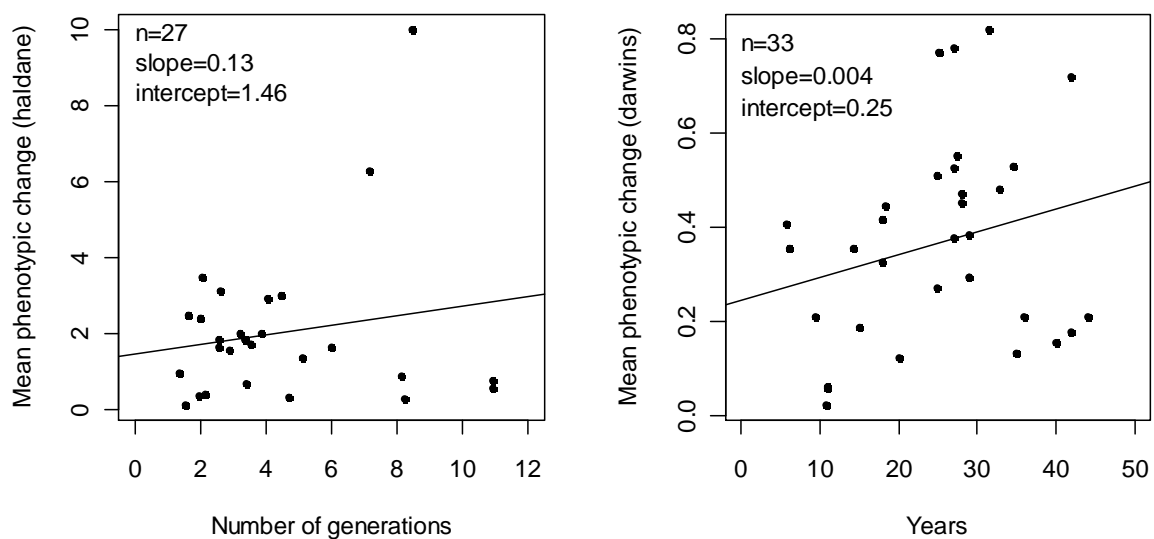


Figure 2. Linear trend in mean phenotypic change for each stock over the number of generations (haldanes) or years (darwins).

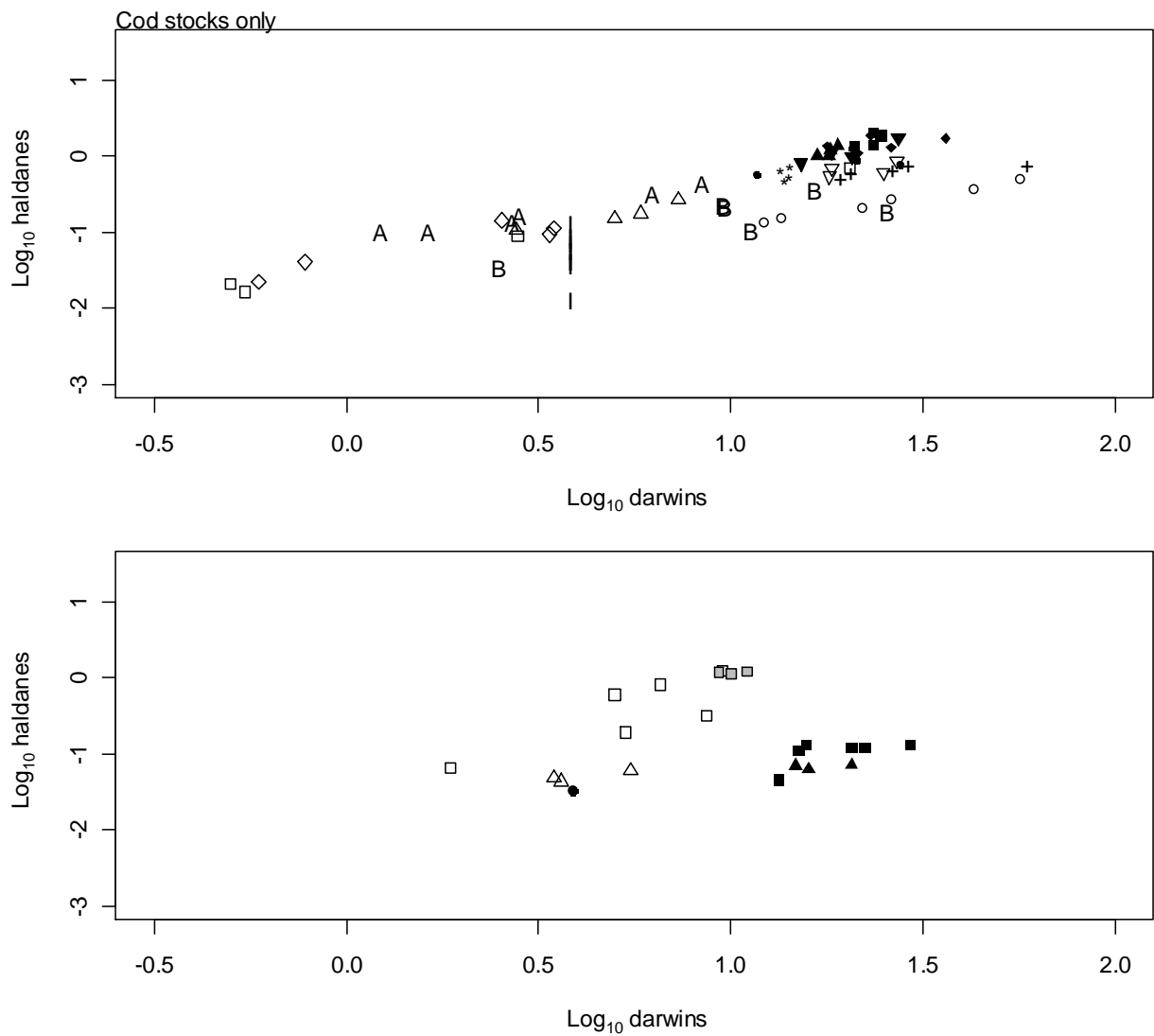


Figure 3. Comparison of estimated rates of evolution specified in log₁₀ darwins and log₁₀ haldanes. Each point represents a single estimate for a given age, sex, and stock. Symbols are defined in Table 1. All rates are expressed as absolute values. Cod stocks were plotted separately (top graph) for clarity.