



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

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## **Interim Report**

**IR-12-036**

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

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#### **Approved by**

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

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14 **Abstract**

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

30

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

33

34 Running title: Rates of evolution in marine fish stocks

35

## 36 INTRODUCTION

37 A wide range of life-history strategies have evolved to maximize life-time reproductive  
38 success under current environmental conditions (Stearns 1992; Hendry and Gonzalez 2008;  
39 Lande 2009). Organisms can become maladapted to their environment as a result of naturally  
40 occurring change; individuals must then either adapt to the new environment through  
41 phenotypic plasticity or evolution, or decline and face extinction (Hendry and Gonzalez  
42 2008; Hendry et al. 2011). Because background environmental variation is typically not  
43 characterized by dramatic or abrupt changes, strong natural selection tends to be uncommon  
44 (Kingsolver et al. 2001), thus, the adaptation process is regarded as being relatively slow  
45 under natural variation. However, rapid or contemporary evolution, defined as significant  
46 trait evolution in less than a few hundred generations (Hendry and Kinnison 1999), is  
47 increasingly observed. Examples include populations adapting to natural or anthropogenic  
48 environmental variation, but the principal factor capable of imposing such a strong selective  
49 force appears to be humans (Palumbi 2001; Mace and Purvis 2008; Hendry et al. 2011).  
50 Anthropogenic disturbances often occur rapidly and include novel stressors thereby  
51 necessitating swift, although often unpredictable, responses (Mace and Purvis 2008; Crispo et  
52 al. 2010). Hendry et al. (2008) found that rates of phenotypic trait change from anthropogenic  
53 disturbances were nearly double those from natural environmental perturbations. The  
54 selective force on traits is thought to be especially strong if it arises from hunting or  
55 harvesting (Darimont et al. 2009) due to the immediate selection for a particular trait, such as  
56 large size or large antlers and horns, coupled with a demographic effect (Coltman et al. 2003;  
57 Allendorf and Hard 2009; Hendry et al. 2011). Phenotypic changes from harvesting were  
58 found to be greater than natural and other anthropogenic disturbances by factors of 3.4 and  
59 1.5, respectively (Darimont et al. 2009).

60 A number of studies have shown that exploitation is capable of inducing evolutionary  
61 changes in behaviour, morphology, and life-history characteristics when the selected  
62 phenotype has a partial genetic basis for large mammals (Coltman et al. 2003; Proaktor et al.  
63 2007) and fish (reviewed by Law 2007; Dunlop et al. 2009; Sharpe and Hendry 2009).  
64 Exploited fish stocks typically show truncated size and age distributions (Longhurst 2002;  
65 Hutchings and Baum 2005; Hsieh et al. 2010) as a direct consequence of increased mortality,  
66 facilitated by the size-selective nature of most fisheries, where the likelihood of capture  
67 increases with size. Intensive harvesting, whether size-selective or not, tends to favour  
68 genotypes with earlier maturation (Law and Grey 1989; Allendorf and Hard 2009) and may  
69 have unforeseen consequences for the entire community (Jennings and Kaiser 1998; Heino  
70 and Godø 2002; Coltman et al. 2003). Sustainable exploitation depends upon sustaining yield  
71 over time, yet harvesting of only those individuals with desirable traits, such as large size,  
72 creates an unnatural selection that is at odds with sustainability (Jørgensen et al. 2007;  
73 Coltman 2008; Allendorf and Hard 2009). Changes in yield and productivity can be linked  
74 back to changes in life-history traits, such as growth rate, length and age at maturation, and  
75 fecundity (Law and Grey 1989; Conover and Munch 2002; Stergiou 2002). [Although  
76 evolutionary changes may be reversible, the long and impractical time frames needed for  
77 reversal are not at the appropriate scale for current management](#) policies (de Roos et al. 2006;  
78 Conover et al. 2009; Enberg et al. 2009). Andersen and Brander (2009) suggested that  
79 fisheries-induced evolution is too slow to warrant attention by managers, but management  
80 should be concerned if the rate of change is fast, i.e., on the scale of years or few decades as  
81 opposed to over hundreds of years (e.g., Law 2007).

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

85 2007; Sharpe and Hendry 2009), have typically been quantified in darwins (Haldane 1949).  
86 The darwin represents the relative rate of change on an absolute time scale (in units of  $e$  per  
87 million years) and is useful when measuring change that is relevant to time-dependent human  
88 interests (Hendry and Kinnison 1999). The ease of estimation is its foremost advantage.  
89 However, the darwin was not developed for quantifying rates of contemporary evolution; the  
90 intended application was for long temporal scales, i.e., morphological traits from the fossil  
91 record (Hendry and Kinnison 1999; Roopnarine 2003). Furthermore, the darwin is influenced  
92 by trait dimensionality; rate comparisons between populations with different generation times  
93 can be misleading, and it is useful solely for ratio scale data, where the scale has a precise  
94 zero point corresponding to a null quantity (Gingerich 1993; Hendry and Kinnison 1999).

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



110 1993). However, comparisons of the two metrics should provide insight into common  
111 evolutionary patterns because .. (Gingerich 2001; Kinnison and Hendry 2001).

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

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

135 2009), by incorporating other factors directly into the maturation reaction norm estimation  
136 (Devine and Heino 2011; Wright et al. 2011a; Wright et al. 2011b), or through experimental  
137 manipulation (Tobin and Wright 2011). Molecular genetic methods have yet to confirm the  
138 evolutionary nature of these changes, but the overriding conclusion of many of the maturation  
139 reaction norm studies was that phenotypic changes likely had a genetic component.

140 Several review papers have used PMRN data to assess rates in darwins (Jørgensen et al.  
141 2007; Darimont et al. 2009; Sharpe and Hendry 2009), but the difficulty in estimating  
142 phenotypic standard deviation has hampered assessment in haldanes. The haldane rates we  
143 estimate are new for most stocks (Olsen et al. (2004) has previously estimated haldanes  
144 describing fisheries-induced evolution), and this is the first comparative study to utilize  
145 haldane rates in our context. Here, we estimate evolutionary rates for twenty-six fish stocks,  
146 mainly gadoids and flatfish, from the Pacific, North Atlantic, Barents Sea, Eastern Baltic, and  
147 the North Sea. Many of these stocks currently support fisheries, while others have been under  
148 moratorium for almost two decades. We assessed whether (1) putative fisheries-induced  
149 evolution qualifies as being fast using two rate metrics, the easily-calculated darwins and the  
150 more refined haldanes, (2) a deterministic pattern is apparent in the evolutionary trajectory of  
151 haldane rates, and (3) the speed of evolution can be correlated with total mortality and  
152 somatic growth.

## 153 **METHODS**

### 154 **Data collection**

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

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

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

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

## 188 **Evolutionary rates**

189 Darwins ( $d$ ) were estimated as:

$$190 \quad (1) \quad d = \frac{\ln(x_1/x_0)}{\Delta t \times 10^{-6}},$$

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

196 Haldanes ( $h$ ), the rate of change in standard deviations per generation, were estimated  
197 using the procedure outlined by Gingerich (1993), with correction by Hendry and Kinnison  
198 (1999) as:

$$199 \quad (2) \quad h = \frac{(x_1 - x_0)/s_p}{g},$$

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

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

216 (3) 
$$s_p = \frac{\pi}{\sqrt{3}\beta_s},$$

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

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

228 (4) 
$$t_g \approx \frac{\sum_t^{t_{max}} t \times S_t \times M_t \times W_t}{\sum_t^{t_{max}} S_t \times M_t \times W_t},$$

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

237 We used the LRI analysis (log-rate versus log-interval; Gingerich 2001; 2009) to assess  
 238 whether evolutionary rates in length at maturation could be considered random, directional,  
 239 or stationary. Gingerich (1993) showed that the slope from a log-rate versus log-interval  
 240 (LRI) relationship, where rates were estimated over multiple time intervals (e.g., over one  
 241 generation, 2-generations, 3-generations), could be used to indicate stasis or stabilizing  
 242 processes (slope = -1.0), randomness (slope = -0.5) or directional change (slope = 0). Rates  
 243 within our dataset were not strictly independent, i.e. rates were from males and females and  
 244 different age cohorts in the same stock. To reduce non-independence, one rate for each stock  
 245 should be chosen, however, the decision of which age or sex to use would likely be arbitrary.  
 246 We used an alternative way of dealing with non-independence and pseudoreplication: we  
 247 used a linear mixed effects model (LME) to test the relationship between absolute rate in  
 248 haldanes and the number of generations (time interval), and included stock + period (all, pre-  
 249 or post-moratorium) as a random intercept term, and assumed a Gaussian distribution for the  
 250 error term. The random intercept term implies that the estimated evolutionary rates for each

251 age class and sex within a single stock (or subpopulation) were most likely correlated.  
252 Absolute rates were used because the direction of change was not relevant in comparing the  
253 relative speed between stocks. Absolute values may artificially inflate the observed change as  
254 a result of measurement error, however, the bias is small if the contribution of measurement  
255 error is similar for all indices (Hendry and Gonzalez 2008) or if the estimated slope is  
256 significantly different from zero (Hereford et al. 2004). Generational rates (*h<sub>0</sub>*) were  
257 estimated from the intercept of the regression of  $\log_{10}$ -rate on  $\log_{10}$ -interval (Gingerich 2009).  
258 Parameters were bootstrapped to obtain 95% confidence intervals. This analysis was not  
259 performed for darwins because the LRI method assesses trait change on a generational basis.  
260 All LME models were fit in R (R Development Core Team 2011), using the lme4 package  
261 (Bates et al. 2011).

262 Evolutionary rates are not independent of the time interval over which they are measured.  
263 Short timescales tend to capture dramatic changes, whereby the initial response to a  
264 perturbation is large and fast and slows with increasing time after the disturbance (Reznick et  
265 al. 1997; Kinnison and Hendry 2001; Hendry et al. 2008). This decline with increasing time  
266 is an artefact of the negative self-correlation caused when rates that have time in the  
267 denominator are compared with time (Sheets and Mitchell 2001). The importance of this self-  
268 correlation was investigated in two ways: 1) by randomizing the rate numerator (trait  
269 difference) with respect to the denominator and inspecting the correlation of the randomized  
270 rate versus the original rate estimate, and 2) by inspecting the numerator or the rate estimate  
271 against time interval. Randomizing the numerator and re-estimating rates should eliminate the  
272 correlation, but a strong negative correlation approximating the actual pattern is often still  
273 apparent (Sheets and Mitchell 2001). If significant autocorrelation within the data exists, the  
274 underlying trend can nevertheless still be examined by testing if the slope and intercept differ  
275 from those estimated from the randomizations (Kinnison and Hendry 2001). Analysing the

276 haldane numerator  $((x_1-x_0)/s_p)$ , which is the total phenotypic change in multiples of  
277 phenotypic standard deviation, removes time from the rate estimation, thereby circumventing  
278 some of the intrinsic self-correlation; rates of phenotypic change can then be compared  
279 against time. When analyzing phenotypic change, untransformed data are typically used, but  
280 the untransformed data here indicated heteroscedasticity. Since violation of this assumption  
281 has the greatest bias on p-values, transformed data were used, but  $\log_{10}$ -transformed data tend  
282 to be influenced by short time intervals (Kinnison and Hendry 2001; Hendry et al. 2008).  
283 Both the average and maximum absolute phenotypic change for a particular sex-stock-trait  
284 combination was used as an estimate of the average and maximum amount of change that  
285 might be accomplished. The use of one value per sex and stock avoided most of the non-  
286 independence issues of using multiple data points within a system. Because we chose to  
287 include data on both sexes within a stock, LME models were again used with a unique stock  
288 + period identifier as a random intercept term and a Gaussian distribution for the error term.

### 289 **Mortality and growth rates**

290 Total mortality rates ( $Z$ ,  $\text{year}^{-1}$ ), were used to investigate the relationship between rates of  
291 evolution and all sources of mortality in the environment. Total mortality includes the direct  
292 effect of fishing (Beverton and Holt 1957), unaccounted mortality, such as that from escape  
293 and discard mortalities, and other unknown mortalities (e.g., predation), which are often  
294 reflected as part of the natural mortality component (Chopin et al. 1996). Rates were  
295 estimated from the change in abundance with age for each year class, using data gathered  
296 from stock assessment reports (Table 1). We did not quantify size dependence of fishing or  
297 total mortality, but we note that management of all fish stocks in our study includes minimum  
298 landing size or minimum mesh size regulations. The mortality regime of the previous  
299 generation will affect life-history traits in the current generation. Therefore, a lag was  
300 introduced by including mean mortality rates up to one generation before the end of the trait



301 time period, i.e., for North Sea sole, change in maturation was estimated for cohorts 1964–  
302 1996 and generation time was 3.8 years, therefore, mean mortality from 1960–1992 was  
303 used. For stocks under moratoria, the lag in total mortality was one generation after  
304 enactment of the moratorium.

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

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

323 Because growth rate can affect other traits, such as survivorship, age at maturity, and  
324 reproductive output (Stearns 1992; Law 2007; Waples and Naish 2009), and variation in  
325 growth may be a reflection of variation in the abiotic and biotic environment, it was used as

326 an indicator of stock productivity. Growth rates may vary as a result of density-dependence  
327 or environmentally driven changes in individual growth (Trippel 1995). Growth rate was  
328 estimated from the Gompertz growth curve:

329 (5) 
$$W(t) = W_{\infty} \exp\left[-\frac{\lambda}{K} e^{-Kt}\right],$$

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

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

## 349 **RESULTS**

## 350 **Evolutionary rates**

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

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

370 For stocks that included environmental factors as covariates within the original PMRN  
371 models, evolutionary rates were within the range exhibited by all stocks (see supplemental  
372 material). Mean rates were significantly different when comparing pre- and post-moratorium  
373 stocks (haldanes and darwins,  $p < 0.001$ ). The pre-moratoria rates of the Northern cod stocks  
374 (2J3KL) were 60%–95% faster than post-moratoria rates. For Southern Gulf of St. Lawrence

375 cod, the differences were less pronounced (23–28% faster than post-moratoria for males, 63–  
376 67% for females). Rates of change for weight at maturation in North Sea sole were  
377 significantly faster than for length at maturation ( $p_{\text{haldane}} = 0.05$ ;  $p_{\text{darwin}} = 0.01$ ). Sample size  
378 was too low to test if rates for chum salmon pre- and post-closure of the high seas gillnet  
379 fishery were significantly different, but post-closure rates were higher than pre-closure  
380 (Figure 2, Table 1).

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

389 Using the LRI approach, the regression of log-rate on log-interval yielded a slope  
390 indicative of random change (slope = -0.68). The slope was significantly different from 0 and  
391 -1 ( $p < 0.001$ ), indicating neither directional change nor stasis was taking place (Figure 2).  
392 However, the bootstrapped (bias corrected) 95% confidence interval was wide (-0.91, -0.48).  
393 The predicted generational rate ( $h_0$ ) of the haldane was 0.56, with a confidence interval  
394 ranging from 0.41 to 0.87.

395 The inverse relationship between rates and time interval was clear (Figure 2).  
396 Correlations between the  $\log_{10}$  rate and  $\log_{10}$  interval for the data were significant for both  
397 haldanes and darwins ( $r_{\text{haldane}} = -0.42$ ;  $r_{\text{darwin}} = -0.28$ ;  $p < 0.001$  for both), indicating rates were  
398 negatively correlated with the length of time over which they were measured. Rate  
399 numerators were randomized with respect to denominators (time interval) to inspect the

400 autocorrelation pattern (Figure 2). Correlations between the rate and interval for the  
401 randomized data were significant ( $r_{\text{haldane}} = -0.46$ ,  $r_{\text{darwin}} = -0.51$ ,  $p < 0.0001$  for both),  
402 indicating high autocorrelation still remained within the data. The underlying trend was  
403 assessed by examining whether the slope and intercept from the actual data differed from  
404 those estimated from a large number of randomizations. For rates in both haldanes and  
405 darwins, the slopes estimated from the data were significantly flatter ( $p < 0.001$ ) and the  
406 intercepts smaller ( $p < 0.001$ ) than those estimated from 1000 randomizations, indicating that  
407 shorter time intervals were associated with small amounts of trait change.

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

#### 414 **Total mortality and growth rates**

415 Rates of trait evolution in gadoids increased with increasing mortality and decreased with  
416 increasing growth rates for haldanes, whereas only mortality had a significant effect on  
417 darwins (Table 3). Fast haldane rates were apparent even under moderate growth ( $K = 0.2 \text{ yr}^{-1}$ )  
418 <sup>1)</sup> for stocks experiencing high total mortality (Figure 4). Under moderately high total  
419 mortality, haldane rates declined as growth rates increased; this effect was obvious when  $Z \leq$   
420  $1.0 \text{ yr}^{-1}$ . Rates in darwins increased with increased mortality (Figure 5).

#### 421 **DISCUSSION**

422 By estimating rates of evolutionary change for life-history traits of exploited fish stocks  
423 across the North Atlantic, Barents Sea, Baltic Sea, North Sea, and Pacific, we have shown

424 that 1) rates of evolution measured in haldanes and darwins were relatively fast, 2)  
425 generational rates were generally fast, and 3) larger phenotypic changes were apparent over  
426 longer time periods for darwins, but not for haldanes. Evolutionary rates and the amount of  
427 phenotypic change in life-history traits, namely length and weight at maturation, were similar  
428 or faster than those for species under anthropogenic disturbance published elsewhere (e.g.,  
429 Hendry et al. 2008; Darimont et al. 2009; Crispo et al. 2010). Phenotypic changes due to  
430 anthropogenic change have been shown to be as high as 6–8 standard deviation units in wild  
431 populations (Hendry et al. 2008; Crispo et al. 2010), while experimental studies on small  
432 populations under strong selection have shown that the mean phenotype could be altered by  
433 several standard deviations within a relatively small number of generations (Falconer and  
434 MacKay 1996). We estimated changes as high as 14 standard deviations in wild marine fish  
435 populations under relatively high harvesting pressure, although most were typically around 2  
436 standard deviation units. Rates estimated here may have been faster than those for  
437 anthropogenic disturbances elsewhere for two reasons. The faster rates may, in part, be a  
438 reflection of the shorter time interval over which we estimated change; a maximum time  
439 interval of 13 generations (or 73 years) as opposed to over 80 generations (or 150 years)  
440 (ref?). Dramatic changes are often captured by short timescales, where the initial response to  
441 the perturbation is large and slows with increasing time from the disturbance (Stockwell et al.  
442 2003). Data were from PMRN studies, which dissociate some of the variability in growth and  
443 mortality from other sources of variation involved in the maturation process, whereas other  
444 rate estimates retain these influences on phenotypic expression of traits. Nevertheless, our  
445 results support earlier evidence that phenotypic change in populations associated with  
446 anthropogenic disturbance is typically faster than for those under only natural selection  
447 (Hendry et al. 2008; Darimont et al. 2009; Crispo et al. 2010).

448       Generational rates of 0.1 to 0.3 standard deviations per generation are considered fast  
449 when compared to the range of possible phenotypes, but not unusual (Gingerich 1993; 2009),  
450 and have contributed to the altered perception of the pace at which evolution can, and does,  
451 occur. Whether rapidity is in fact frequently encountered in nature, but not reported, has also  
452 been questioned (Hairston et al. 2005). The generational rate of change in haldanes ( $h_0$ ) for  
453 fish stocks presented here was 0.6 standard deviations per generation. This is in agreement  
454 with a meta-analysis of 2151 rates by Kinnison and Hendry (2001), indicating that the range  
455 reported by Gingerich (1993, 2009) may be much lower than that typically seen in  
456 populations experiencing human-induced perturbations. It is possible that our high  
457 generational rates may be a result of slight publication bias. Most of the PMRN studies  
458 investigated stocks that showed declines in size at maturation, and very few studies focused  
459 on stocks showing no or little change. If positive and negative rates are analyzed separately in  
460 the manner of Gingerich (2001), the generational rates are 0.51 and 0.54, respectively, and  
461 can still be considered high.

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

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

476 Variations and reversals in evolutionary trajectories are common in many examples of  
477 contemporary evolution (Gingerich 1983; Hendry and Kinnison 1999; Estes and Arnold  
478 2007; Schoener 2011); however, the LRI application indicated that neither stasis nor  
479 directional change was occurring. This was unexpected given that we expected fisheries-  
480 induced selection to cause directional change. Non-random patterns should be apparent if  
481 directional or stabilizing selection is causing trait evolution (Gingerich 1993) and were  
482 expected to be apparent within our data given the selection caused by high exploitation.  
483 Stasis, which is a pattern of multiple reversals or high variability in rates, is thought unlikely  
484 to occur over short intervals (Gingerich 1993; 2001; Kinnison and Hendry 2001), and our  
485 failure to detect a deterministic pattern may be due to the relatively short, less than 5  
486 generations for most stocks and never more than 13 generations, time scale of our study.  
487 Although the LRI application suggested that the rate of change in traits could not be  
488 differentiated from random change, this does not provide definite proof that the change is  
489 random. The non-significant result can be interpreted as an indication that processes are  
490 interacting to produce results that are indistinguishable from randomness, i.e. a slope  
491 approaching random change is often expected in fluctuating environments, but it can also  
492 indicate that a neutral mixture of directional and stabilizing selection processes are occurring  
493 (Roopnarine 2003; Gingerich 2009). Siepielski et al. (2009), in a meta-analysis of 5519  
494 selection estimates from wild populations, found that strong selection is present, but rarely  
495 sustained, and change in direction is common, which will lead to evolutionary rates that  
496 appear to be under random change. Most of the included stocks have been under sustained  
497 fishing pressure, but this does not exclude the possibility that agents of selection other than



498 fishing are also important and observable as randomness in the overall pattern. Another  
499 possibility is that the relatively short time series that dominate the analysis have made the  
500 LRI application more sensitive to measurement error in the raw data.

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

515 The statistical methods currently used to explore life-history trait change, e.g., PMRNs,  
516 do not perfectly disentangle genetic effects from phenotypic plasticity due to environment  
517 (Heino and Dieckmann 2008; Morita et al. 2009; Tobin and Wright 2011). The individual  
518 phenotypic expression of traits is a function of individual genetics and environmental  
519 interactions and as such, disentangling the ecological versus genetic change is difficult to  
520 prove. Furthermore, a widely applicable method for disentangling plastic and evolutionary  
521 effects for traits other than maturation is not available. This highlights the need for

522 indisputable evidence of genetic change. Regardless, imperfect disentanglement does not  
523 make the PMRN approach, nor the evolutionary rates estimated here, invalid.

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

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

547 (Andersen et al. 2007; Sharpe and Hendry 2009). Population characteristics that affect  
548 productivity and yield, such as large size, are often the traits directly selected for by humans,  
549 however, a shift towards earlier maturation will unintentionally lead to smaller average adult  
550 size and eventually to reduced yield (Law and Grey 1989; Heino 1998; Conover and Munch  
551 2002). Management strategies typically aim to sustain yield in the short-term and including  
552 evolutionary considerations into fishery management plans, although acknowledged for  
553 decades (e.g., Stokes et al. 1993), has only recently been highlighted as essential (Jørgensen  
554 et al. 2007). Possible scenarios suggested to slow the evolutionary effects of fishing include  
555 lowering fishing mortality, enacting maximum and minimum size limits, or restricting fishing  
556 to certain areas through the use of marine protected areas or temporary closures (Baskett et al.  
557 2005; Andersen et al. 2007; Hutchings 2009). A decrease in mortality significantly and  
558 rapidly slowed the rate of evolution in size at maturation for cod stocks in the Northwest  
559 Atlantic, and has been shown to have beneficial effects on other life history traits, such as  
560 growth and reproduction, in the short term (Rochet 1998; Andersen et al. 2007). It has been  
561 argued that the genetic effects of fishing on age and size at maturation will be slow to reverse  
562 and practically irreversible (Law and Grey 1989; Dunlop et al. 2009; Enberg et al. 2009);  
563 however, recent experimental studies have shown that the detrimental evolutionary effects of  
564 size-selective harvest can, in some cases, be overturned if sufficient genetic variation remains  
565 in the population (Conover et al. 2009). Whether this is the case for Northwest Atlantic cod  
566 stocks or if the rapid changes detected are an artefact of the short time scale is unclear.  
567 Regardless, recovery is difficult to predict without sufficient knowledge of extrinsic  
568 environmental factors capable of applying selective pressure or how these factors may  
569 influence life history characteristics under exploitation (Enberg et al. 2009).

570 Coltman (2008) found that even a modest exploitation rate can have a significant genetic  
571 impact on the target population when viewed on an ecological time scale. However, Hairston

572 et al. (2005) argue that the speed of evolutionary change matters in an ecological context only  
573 if it is fast enough to alter the outcomes of ecological interactions. The effects of evolving  
574 life-history traits on population and community dynamics have been well reviewed and  
575 include modified predator-prey and competitive dynamics, amplified responses due to  
576 mutually reinforced correlations between traits, and changes in growth, condition,  
577 reproductive output and, ultimately, yield and productivity (Kuparinen and Merilä 2007; Law  
578 2007; Coltman 2008; Hutchings and Fraser 2008). The comparable, but relatively fast, rates  
579 of contemporary evolution estimated in this study can be viewed as a positive response to the  
580 changing selection pressures imposed by decades of commercial fishing if we consider it as  
581 the ability of a stock or species to avoid extinction (Kaitala and Getz 1995; Heino 1998;  
582 Enberg et al. 2009). Given the potential for cascading negative consequences of life-history  
583 evolution on ecological time scales, there is a pressing need to determine and implement  
584 strategies that will mitigate these effects whilst maintaining sustainable fisheries and basic  
585 ecosystem services.

586 In conclusion, changes in life-history characteristics for exploited fish populations are  
587 occurring at a rapid rate, but have the potential to slow with increasing growth rates and  
588 declining mortality rates. Our results support the hypothesis that fishing is an important driver  
589 of life-history change in fish, in agreement with an earlier analysis by Sharpe and Hendry  
590 (2009). However, because most of the studies included here did not explicitly investigate the  
591 effect of environment on trait change (beyond the growth and survival effects accounted for  
592 by the PMRN method), we cannot rule out the possibility that the observed changes are, in  
593 part, due to environmental change. Regardless of primary causes, trait evolution is occurring  
594 and it will have repercussions for stock demographics, productivity, recovery and, ultimately,  
595 economic yield. Evolutionarily enlightened management considers both the ecological and  
596 evolutionary consequences of fishing, but fisheries management has been slow to

597 acknowledge that characteristics of fish populations can change over time. The effect of  
598 changing traits, whether of evolutionary nature or not, has been poorly integrated into the  
599 fisheries assessment process, except in a few notable examples (e.g., Scott et al. 1999;  
600 Marshall et al. 2000; Marshall et al. 2006). By incorporating trait changes into the  
601 recruitment process, future changes in productivity can be modeled and resilience to  
602 exploitation or perturbations, such as climate change, can be explored. Furthermore,  
603 evolutionarily enlightened management needs not to be a passive observer of evolution, but  
604 could pursue strategies to slow unwanted trait evolution, for example by shifting from  
605 strategies maximizing yield towards those that protect the age and size distribution of the  
606 population.

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870



871 **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**  
872 **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**  
873 **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**  
874 **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-**  
875 **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**  
876 **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<sub>50</sub> and Wp<sub>50</sub> rates for**  
877 **North Sea sole. Rates for males can be found in the Supplemental Material.**

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

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

**Common sole, *Solea solea*, Soleidae**

▲, Δ	North Sea <sup>14</sup>	(ICES 2009a)	1960–2002	2–4	10.9	Regression	0.05, 0.07	4.2, 17.1	decrease
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**Chum salmon, *Oncorhynchus keta*, Salmonidae**

									decrease,
C, c	Chitose River, Japan <sup>15</sup>	–	1973–1993	4	3.3, 2.1	–	0.21, 0.78	6.4, 23.9	increase
									decrease,
*, *	Nishibetsu River, Japan <sup>15</sup>	–	1973–1993	4	3.2, 2.0	–	0.17, 0.53	6.4, 23.9	increase
									decrease,
T, t	Tokachi River, Japan <sup>15</sup>	–	1973–1993	4	2.9, 1.8	–	0.09, 0.75	4.7, 26.5	increase

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878 References for traits: <sup>1</sup> M. Heino, unpublished data; <sup>2</sup> Pardoe et al. (2009); <sup>3</sup> Vainikka et al. (2009); <sup>4</sup> L. Marty, unpublished data, including maturity ogives; <sup>5</sup> Wright et al.  
879 (2011b); including maturity ogives; <sup>6</sup> L. Baulier, unpublished data; <sup>7</sup> Swain (2011); <sup>8</sup> Barot et al. (2004b); <sup>9</sup> Wright et al. (2011a), males only; <sup>10</sup> Devine and Heino (2011); <sup>11</sup>  
880 Enberg and Heino (2007); <sup>12</sup> Barot et al. (2005); <sup>13</sup> van Walraven et al. (2010); <sup>14</sup> Mollet et al. (2007), including maturity ogives; <sup>15</sup> Fukuwaka and Morita (2008).

881 **Table 2. Results of regression through log<sub>10</sub>-transformed rates of mean and maximum phenotypic change**  
 882 **(i.e., the rate numerator) in haldanes and darwins over time interval, including 95% confidence intervals**  
 883 **(CI) of the slope.**

Model	Slope	Intercept	n	95% CI (slope)
<b>Haldanes</b>				
Mean	0.09	-0.08	58	-0.15, 0.46
Maximum	0.07	0.02	58	-0.16, 0.42
<b>Darwins</b>				
Mean	0.62	4.58	64	0.31, 1.07
Maximum	0.70	4.45	64	0.36, 1.18

884

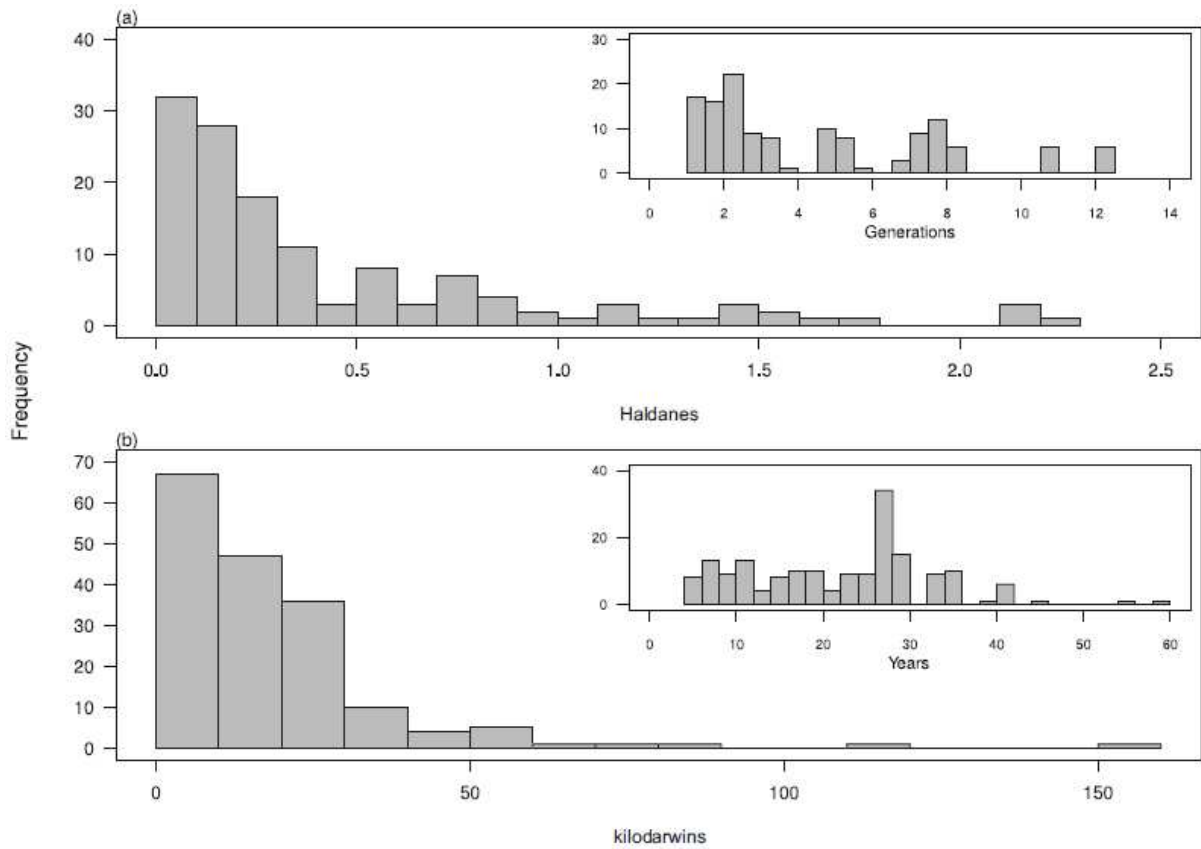
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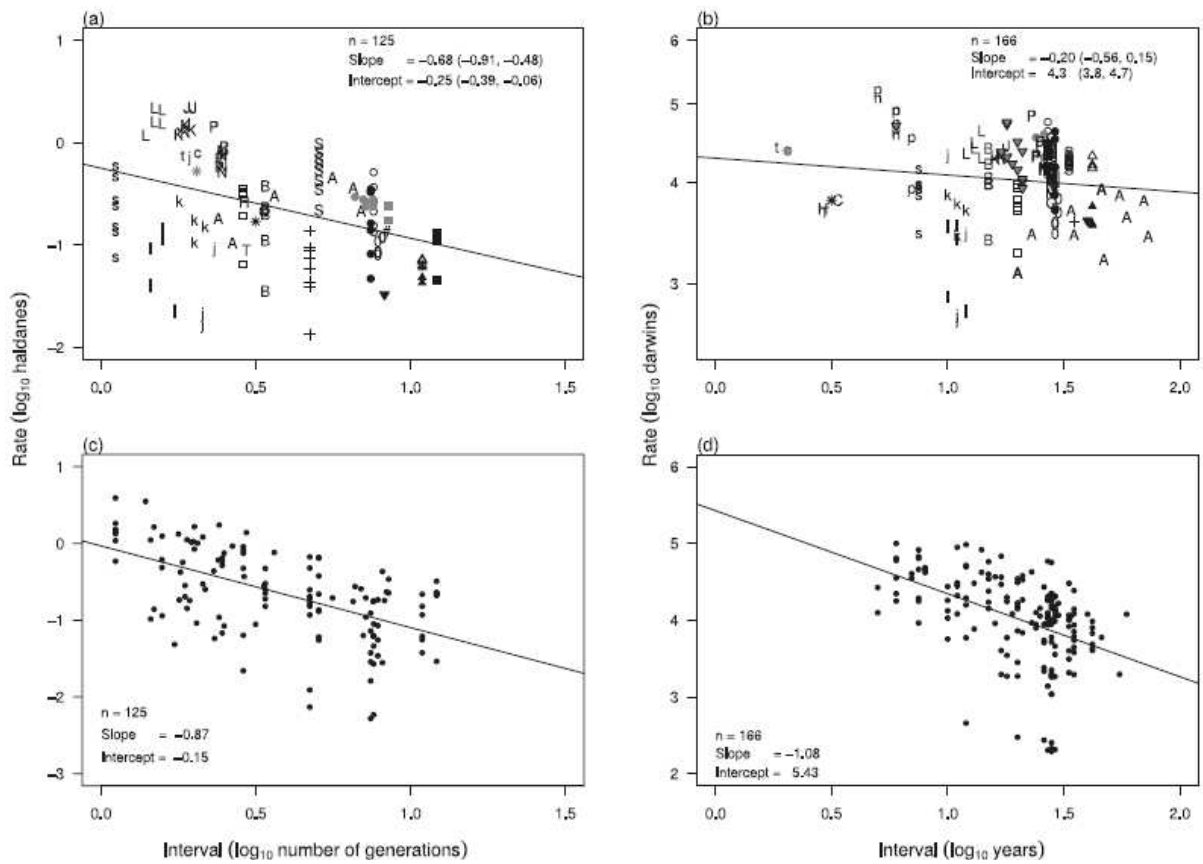
887 **Table 3. Effect of total mortality and somatic growth on absolute rates of trait evolution in haldanes and**  
 888 **darwins as fit by GAMMs.**

Model	Effect of rate	F	N	p-value
<b>Haldanes</b>				
Mortality (Z, yr <sup>-1</sup> )	Positive	6.3	44	0.02
Growth (K, yr <sup>-1</sup> )	Negative	5.3	44	0.01
<b>Darwins</b>				
Mortality (Z, yr <sup>-1</sup> )	Negative	6.3	44	0.02
Growth (K, yr <sup>-1</sup> )	Not significant	–	–	–

889



890  
 891 Figure 1. Histogram of absolute rates for haldanes (top) and Kdarwins (bottom) for life-  
 892 history characteristics estimated from PMRN studies. Inserts are histograms of the number of  
 893 generations (haldanes) and years (darwins).



894

895 Figure 2. (top) Evolutionary rates in haldanes (left) and darwins (right) plotted as  $\log_{10}$  rates

896 over  $\log_{10}$  time interval in number of generations (haldanes) or years (darwins). Each point

897 represents a single rate for a stock-age-sex-trait combination; symbol definition is in Table 1.

898 Because rates tend to scale negatively with time, a trend line, estimated from a linear mixed

899 effects model where stock + period was included as a random effect, is shown so that rates

900 faster or slower than the mean predicted value can be evaluated. (bottom) Randomized log-

901 rate versus log-interval (LRI) plot for haldanes (left) and darwins (right), where numerators

902 were randomized with respect to the number of generations or years (see Kinnison and

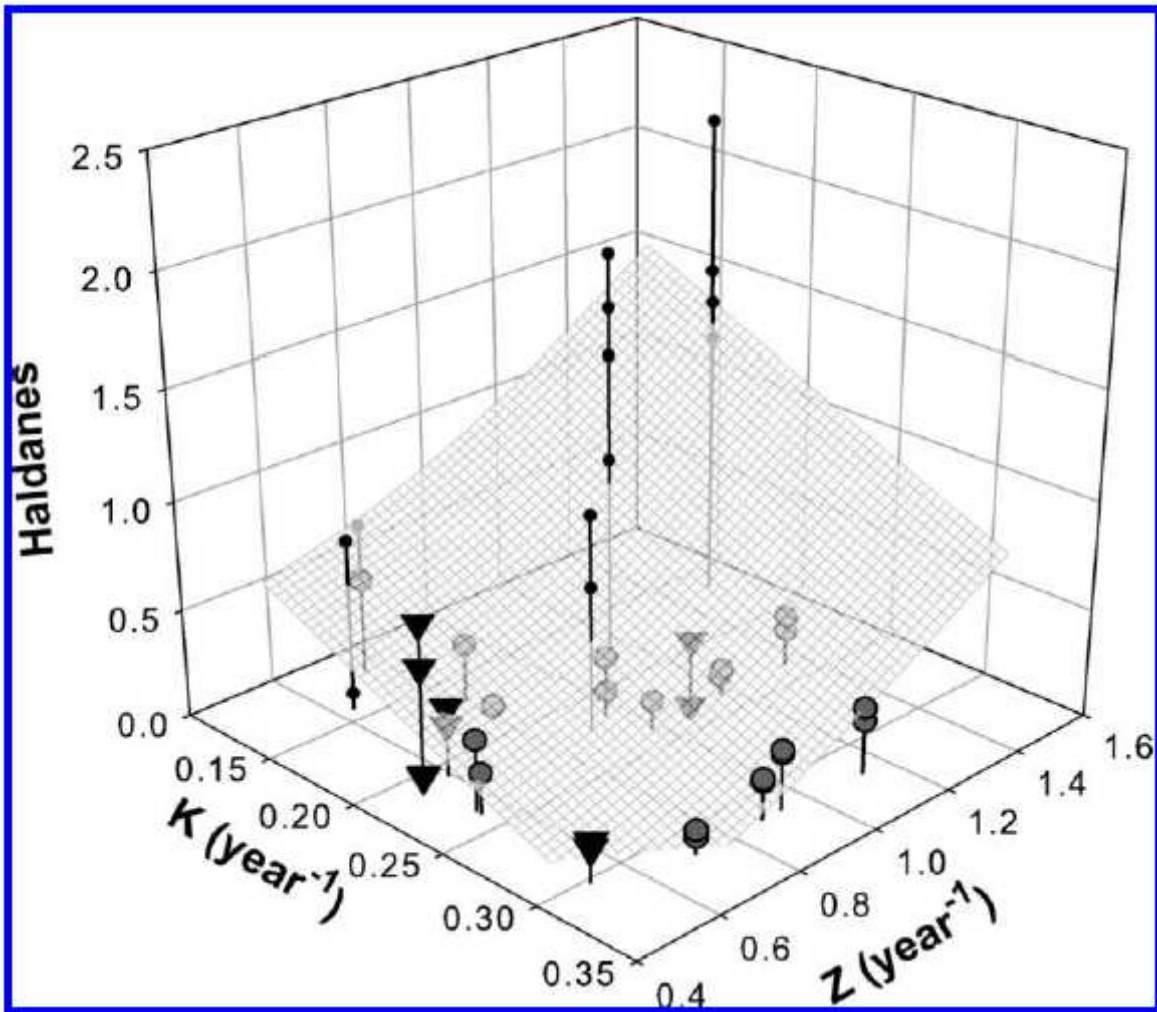
903 Hendry 2001). All rates were expressed as absolute values as the direction of change was not

904 relevant in comparing the relative speed of trait change between stocks. Cod stocks 3NO and

905 3Ps, where the number of generations was  $< 1$ , were not included in the haldane plots.

906

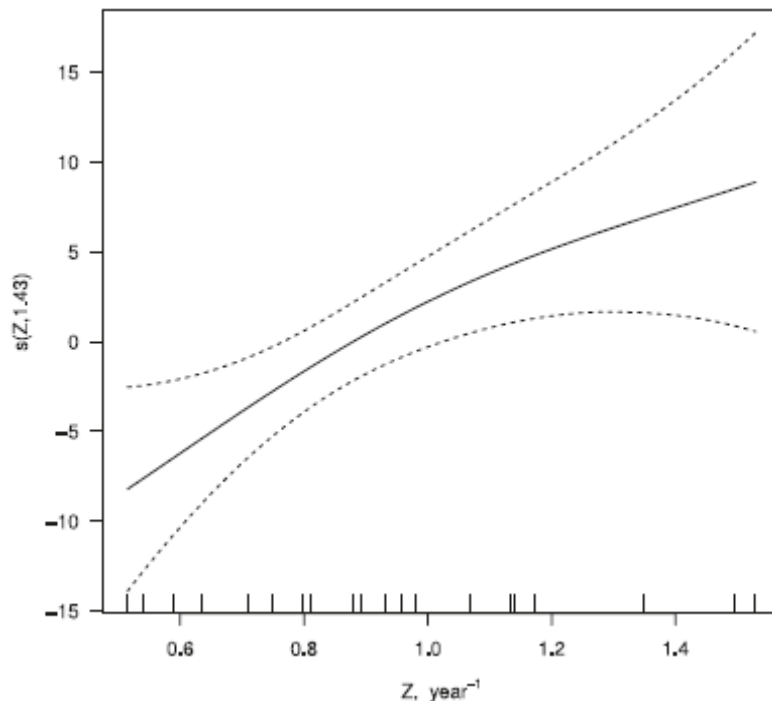




912

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





916

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