

## Article (refereed)

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Edeline, Eric; Le Rouzic, Arnaud; **Winfield, Ian J.; Fletcher, Janice M.; James, J. Ben**; Stenseth, Nils Chr.; Vollestad, L. Asbjorn. 2009 Harvest-induced disruptive selection increases variance in fitness-related traits. *Proceedings of the Royal Society of London, B*, 276 (1676). 4163-4171. [10.1098/rspb.2009.1106](https://doi.org/10.1098/rspb.2009.1106)

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# Title: **Harvest-induced disruptive selection increases variance in fitness-related traits**

Running title: **Diversifying fishery selection**

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Word count: Abstract:	198
Main text:	5,063
Number of references:	37
Number of figures:	4
Number of tables:	3

**KEY WORDS:** Adaptive landscape, Conservation, Contemporary life-history evolution, Evolvability, Nonlinear selection.

**ABSTRACT:**

The form of Darwinian selection has important ecological and management implications. Negative effects of harvesting are often ascribed to size truncation and resultant decrease in trait variability, which depresses capacity to buffer environmental change, hinders evolutionary rebound and ultimately impairs population recovery. However, the exact form of harvest-induced selection is generally unknown and the effects of harvest on trait variability remain unexplored. Here we use unique data from the Windermere (UK) long-term ecological experiment to show in a top predator (pike *Esox lucius*) that the fishery does not induce size truncation but disruptive (diversifying) selection, and does not decrease but rather increases variability in pike somatic growth rate and size-at-age. This result is supported by complementary modeling approaches removing the effects of catch selectivity, selection prior to the catch, and environmental variation. Therefore, fishing most likely increased genetic variability for somatic growth in pike and presumably favoured an observed rapid evolutionary rebound after fishery relaxation. The common *a priori* assumption that harvesting induces size truncation and decreased trait variability may lead to false inference about the mechanisms through which harvesting negatively affects population numbers and recovery. From a management perspective, disruptive harvesting necessitates combining a preservation of large individuals with moderate exploitation rates and thus provides a comprehensive tool for sustainable exploitation of natural resources.

**KEY WORDS:** Adaptive landscape, Conservation, Contemporary life-history evolution, Evolvability, Nonlinear selection.

## INTRODUCTION

Humans are tremendously strong agents of Darwinian selection. Evolutionary change in response to human activities is best documented in harvested systems where selective removal of large individuals by fishers, hunters and plant harvesters rapidly reduces mean body size and mean age at maturity (Haugen2001)(Conover2002)(Coltman2003)(Law2005)(Edeline2007#1611). Maybe due to a focus on mean trait values, harvest-induced selection is almost systematically equated to strict size truncation, i.e., the removal of *all* individuals larger than a limit size (Jørgensen2007)(Conover2002)(Berkeley2004)(Hutchings2005)(Hsieh2006)(Hutchings2008), and many of the negative effects of harvesting to population persistence and recovery are ascribed to size truncation (Berkeley2004)(Hsieh2006)(Hutchings2008). Truncation selection against large individuals is particularly detrimental to exploited populations because older and larger individuals often produce more and higher quality offspring than younger, smaller individuals (Berkeley2004)(Hutchings2005). Hence, selective harvesting of large individuals affects population rate of increase more negatively than would do random harvesting. Additionally, truncation selection erodes genetic variance (Roff1997) and could thus cause irreversible trait changes because genetic variability is necessary for selection to act on (Hutchings2008). In particular, artificial size truncation acting in directional opposition with natural selection (Edeline2007#1611) might induce a more severe reduction in body size variance compared to size truncation acting alone (Conover2009). However, most often the exact form of harvest-induced selection is unknown and the effect of harvesting on trait variability remains unexplored.

Recent studies in Gulf of Saint Lawrence cod *Gadus morhua* (Sinclair2002#1148) and Windermere pike *Esox lucius* (Carlson2007#1537) show that fishery-induced selection is not necessarily truncation selection but can instead be disruptive selection. Disruptive selection

occurs when individuals with intermediate trait values (here body size) have lower fitness than individuals with extreme trait values (Roff1997)(Carlson2007#1537), and disruptive fishing arises from gear selectivity and/or segregation of fish on fishing grounds by size and age. Theory predicts that disruptive selection, in contrast to truncation selection, should increase phenotypic variance, genetic variance and population adaptability. Here we use unique data from the Windermere long-term ecological experiment (Le\_Cren2001) (Winfield2008) to link changes in the strength of disruptive selection from a gillnet scientific fishery to changes in phenotypic variability of Windermere pike. We show that, as predicted by the theory, disruptive fishery selection is associated with increased phenotypic variance in pike somatic growth and size-at-age.

Windermere is a glacial valley lake of the English Lake District (Northwest UK) that has been under extensive scientific monitoring since decades (see Materials and Methods). Natural and fishery-induced selection act in direct opposition on Windermere pike body size (Carlson2007#1537). We illustrate this antagonism between natural and fishery selection in Table 1 and figure 1a, which were built using the same data and methods as Carlson *et al.* (2007) but with a different grouping structure for data (see Materials and Methods). Natural selection acting on Windermere pike body size is stabilizing (intermediate-sized pike have the highest survival probability, Table 1 and figure 1a), became increasingly stabilising over time (figure 1a), and the naturally selected body size optimum is larger than the population mean so that the directional selection gradient is positive (Table 1). The stabilizing form of natural selection presumably reflects the combined effects of cannibalism (Le\_Cren1987) (Haugen2007) and senescence (note that owing to fish asymptotic growth, natural selection acting on age is less stabilizing than natural selection acting on body length (EdelineSubmitted)). In contrast, scientific fishery selection is disruptive (Table 1 and figure

1a), became less disruptive over time (figure 1a), and the fitness valley is also larger than the population mean so that the resulting selection gradient is negative (Table 1). Changes in mean pike somatic growth were driven by the directional antagonism between the two selective forces (Edeline2007#1611). From 1944 to 1963, the strength of fishery selection dominated over the strength of natural selection, resulting in decreased mean individual somatic growth. During this period, exploitation rate increased and the fishery annually removed from 1.1 to 7.3 % (mean 3.3%) of the pike population. From 1963 to 1993, exploitation rate decreased (from 4.95 to 0.13 %, mean 1.1 %) and fishery selection was overridden by natural selection, triggering a rapid increase in mean pike somatic growth. These results have shown that the dominant selective force determined the position of the phenotypic optimum (i.e., drove movements of the adaptive peak on the adaptive landscape). Here our aim was to investigate whether the dominant selective force also drove peak sharpness around the phenotypic optimum (i.e., drove the curvature of the adaptive landscape). We predicted that the dominance of fishery selection over natural selection up the early 1960's should have imposed a concave adaptive landscape and thus favoured an increase in pike phenotypic variance. In contrast, the dominance of natural selection over fishery selection after the early 1960's should have imposed a convex adaptive landscape and thus favoured a decrease in pike phenotypic variance. Our results support these predictions.

## **MATERIALS AND METHODS**

### **Sampling site and data collection**

Pike in Windermere have been sampled each year since 1944 as part of a long-term scientific monitoring program (Winfield2008)(Le\_Cren2001). A spring (March-April) component of this sampling was designed to capture a large size range of pike using shore seines, perch

traps, and 46 and 64 mm gillnets. Note that reduced catchability of larger fish might have influenced our estimation of the shape of natural mortality in Fig. 1a. Captured pike were all measured for total body length (to the nearest cm), tagged and released. Resulting catch-mark-recapture (CMR) data have been extensively described in two recent papers (Haugen2006) (Haugen2007). As part of the scientific program, pike were also sampled in winter (October-February) in a gillnet fishery (64 mm mesh size) which targeted pike longer than 54 cm (Frost1967). All pike captured in the winter fishery were killed, sexed, measured for total body length (to the nearest cm) and the opercular bones were removed for age and length backcalculation following a validated method (Frost1959). Bone density differs between summer and winter, producing narrow bands ("checks") that are deposited on the opercular bones during the slow winter growth period. These checks then serve as an annual mark and, thus, allow the aging of individual fish (Frost1959). An individual's length is back-calculated at each age using a relationship between the radius of the opercular bone at each check and body length (Frost1959). Windermere surface water temperatures (in °C) were recorded on a near daily basis and were here averaged for each year. Finally, the abundance of pike and perch (*Perca fluviatilis*, the main food for pike) have been estimated annually for the 1944-1995 period, separately for each basin as well as separately for young (age = 2) and old individuals (age > 2) (des\_Clers1994).

### **The form and strength of selection**

We estimated the form of selection from survival instead of total fitness (survival\*reproductive success) because (1) no data exists for pike reproductive success, (2) an approximation of reproductive success by fecundity can be made only for female pike because no data exists for fecundity in male pike, and (3) female survival is by far more

critical to population growth than female fecundity in Windermere pike (EdelineSubmitted).

We quantified the age-specific strength and form of natural and fishery-induced selection acting on Windermere pike body size (Table 1, figures 1a and 1b) using previously described procedures based on logistic regressions (Carlson2007#1537). In the CMR data an individual pike tagged in spring of year  $t$  was considered to have survived through the summer of year  $t$  (survival = 1) if recaptured at any point in time after the summer of year  $t$ . This assumption has been validated (Carlson2007#1537). In contrast, a fish that was never recaptured after the summer of year  $t$  was attributed a survival of 0 for this summer. In the fishery data, fish were given a survival of 0 for age and size at capture, and a survival of 1 for previous backcalculated ages and sizes (Sinclair2002#1148). In Table 1, estimates of directional selection gradients acting on body length were obtained using logistic regressions of survival on standardized body length (zero mean and SD of unity), and quadratic selection gradients were obtained using logistic regressions of survival on standardized body length plus its squared term (Janzen1998). We estimated age-specific selection gradients in Table 1 by breaking both datasets into age classes. In the CMR dataset, because only recaptured fish were aged we produced age classes based on the minimum and maximum body lengths of each age-class in the fishery data. For instance, backcalculated length-at-age-1 ranged from 14 to 38 cm, and all fish of length-at-capture ranging from 14 to 38 cm were attributed age 1 in the CMR data. In figures 1a and 1b, we visualized the form of the pike adaptive landscape using natural cubic splines with 9 knots in logistic generalized additive models (mgcv library of the R software (R\_Development\_Core\_Team2008)(Wood2006)(Carlson2007#1537)), i.e., there was no *a priori* assumption about the form of selection. Finally, to model survival as a function of somatic growth in figure 1b, survival at age  $t$  was considered relative to length

increase between age  $t-1$  and age  $t$ , and only fish of length-at-age- $t-1 > 54$  cm were included in the analysis.

### Maximum likelihood estimates of unbiased means and variances

Observed somatic growth distributions in each year class might be distorted pictures of distributions at birth due to natural selection prior to the catch and due to the selectivity of the catch itself. We modeled such possible sampling biases using selection functions from figure 1a as filters to backward estimate unbiased somatic growth rate distributions from sampled distributions. Individual pike lifetime somatic growth rate  $g_i$  was equated to von Bertalanffy's asymptotic length (Edeline2007#1611), which was computed using a nonlinear restricted maximum likelihood (REML) mixed-effects model with a random individual effect in the nlme library of the R software (Pinheiro2000)(R\_Development\_Core\_Team2008). Briefly, Windermere pike growth is best described by the 3 parameters von Bertalanffy growth curve (VBGC) (Ratkowsky1990):

$$l_{g,t} = g_i - 2.93 \cdot g_i \cdot 0.698^t \quad \text{Eq.1,}$$

where  $l_{g,t}$  is the length-at-age- $t$  of fish  $i$  of asymptotic length  $g_i$ , and -2.93 and 0.698 are constants estimated by nonlinear least squares fitting of the VBGC on the whole population. To compute  $g_i$ , Eq.1 was incorporated into a REML linear mixed effects model in which  $g_i$  was associated to a random individual effect  $b_i$  so that  $g_i = \beta_0 + b_i$ , where  $\beta_0$  was model intercept (i.e., population's  $g$ ). The survival probability of fish  $i$  at age  $t$  through natural selection (probability  $s \cdot l_{g,t}$ ) and through fishery selection (probability  $f \cdot l_{g,t}$ ) are known from survival functions (figure 1a). To be caught at age  $c_i$ , a given fish  $i$  has to survive

selection (probability product  $s \square l_{g,t} \square f \square l_{g,t} \square$ ) for  $c_i - 1$  years, and then to survive natural selection one more year before being caught (with probability  $s \square l_{g,c_i} \square \times [1 - f \square l_{g,c_i} \square]$ ). The

likelihood of the particular life history of fish  $i$  can thus be written:

$$L \square m, v \square g_i \square = Pr \square g_i \square \# m, v \square = \frac{b \square g_i \square \# m, v \square \times \left[ \prod_{t=1}^{c_i-1} s \square l_{g,t} \square f \square l_{g,t} \square \right] \times s \square l_{g,c_i} \square \times [1 - f \square l_{g,c_i} \square]}{Surv \square m, v, c_i \square} \quad \text{Eq.2,}$$

where  $m$  and  $v$  are the estimated mean and variance of the normally distributed asymptotic lengths in the population before selection,  $b(g_i | m, v)$  is the probability for an individual of asymptotic length  $g_i$  to be born in a population of mean  $m$  and variance  $v$  for  $g$ .  $Surv(m, v, c_i)$  is the expected survival rate until age of capture  $c_i$  in the whole population such that:

$$Surv \square m, v, c_i \square = \int b \square g \square \# m, v \square \times \left[ \prod_{t=1}^{c_i-1} s \square l_{g,t} \square f \square l_{g,t} \square \right] \times s \square l_{g,c_i} \square \times [1 - f \square l_{g,c_i} \square] dg \quad \text{Eq.3.}$$

The full model, including all  $N$  sampled fish, allows the mean and the variance of the population to be independently estimated for each year class. There are thus two vectors of parameters to estimate:  $\mathbf{M} = (m_{1944}, m_{1945}, \dots, m_{1993})$  and  $\mathbf{V} = (v_{1944}, v_{1945}, \dots, v_{1993})$ . The form and strength of natural selection and fishery selection were allowed to vary according to time (3 periods from 1944 to 1958, from 1959 to 1969, and from 1970 to 1993, see figure 1a). The general likelihood function is:

$$LDM, V \# g_{1 \dots n} = \prod_{i=1}^n PrOgi \# m_i, v_i \quad \text{Eq.4,}$$

where  $y_i$  is the year class of fish  $i$ . Maximum likelihood estimates of reconstructed means and variances, as well as their standard errors, were obtained using the software AD Model Builder (Otto Research Ltd., <http://admb-project.org/>). Reconstructed means were not directly relevant to the present study and are thus provided as an electronic supplementary material (figure S1). We validated the method using simulated data (see below). The simulations stressed that bias removal necessitates large sample sizes (at least a couple of hundred individuals). For this reason, the analysis of real data has been performed by pooling the measures in 5-year bins (figures 1*d* and S1).

The model has been checked using simulated data. Simulations were performed with the R software. 50 cohorts of  $N=100,000$  individuals have been simulated during the 1940 to 1990 period. The growth rate of each individual was sampled from a normal distribution of given mean and variance. To make sure that the simulations explored the whole range of realistic means and variances, a trend has been simulated ("theoretical" lines in figure 2). Each individual of the population then went through a series of survival events; the probability to survive natural selection and fishery depended on the length of the fish (calculated from its age and its asymptotic length  $g_i$ ) and the selection strengths at that time (see figure 1*a*). If the fish was caught (failure to survive the fishery event), it was added to the simulated dataset ("uncorrected" lines in figure 2). Overall, due to strong juvenile selection, between 500 and 1000 fishes were "caught" every year, which is the same order of magnitude as the real dataset. The simulated dataset was analyzed with the same model as the real data to produce "unbiased" lines in figure 2. Proximity between "theoretical" and "unbiased" lines in figure 2 indicates that our model successfully reconstructed somatic growth rate distributions at birth from sampled distributions.

## Trends in residual phenotypic variance

We modeled changes in residual variance for pike lifetime somatic growth rate and length-at-age while statistically accounting for (i) the plastic effects of temperature and food availability on pike growth (Winfield2008)(Kipling1983#1819), (ii) changes in average trait values due to directional selection (Edeline2007#1611), and (iii) temporal trends in residual variance due to nonlinear (i.e., disruptive or stabilizing) selection. We used linear REML mixed-effects models in the nlme library of the R software, which provides built-in functions to explicitly model variance structure of within-group residuals using covariates (Pinheiro2000). Model details are provided in Table 2. To estimate changes in variance for pike lifetime somatic growth rate, we used  $g_i$  as the response in a REML linear mixed-effects model:

$$g_{ij} = \beta_0 + \beta_1 S_i + \beta_2 Bas_i + \beta_3 T_i + \beta_4 Ypi_i + \beta_5 Opi_i + \beta_6 Ype_i + \beta_7 Ope_i + \beta_8 Yc_i + \beta_9 P_i + \beta_{10} T_i \times Ypi_i + \beta_{11} T_i \times Opi_i + \beta_{12} T_i \times Ype_i + \beta_{13} T_i \times Ope_i + \beta_{14} Yc_i \times P_i + b_j \approx_{ij} \quad \text{Eq.5,}$$

where  $\beta_s$  are model coefficients, and fixed effects covariates are as follows:  $S$ =Sex,  $Bas$ =Basin,  $T$ =temperature,  $Ypi$ =density of young pike (age=2),  $Opi$ =density of old pike (age>2),  $Ype$ =density of young perch,  $Ope$ =density of old perch,  $Yc$ =Year class (i.e., cohort),  $P$ =period factor ( $P1$ : Period 1 of dominating fishery selection from 1944 to 1963, and  $P2$ : Period 2 of dominating natural selection from 1964 to 1993). Finally,  $b_j$  is a normally distributed random  $Yc$  effect, nested into  $S$ , nested into  $Bas$  (Table 2), and  $\approx_{ij}$  represents normally distributed within-group residuals. Environmental covariates ( $T$ ,  $Ypi$ ,  $Opi$ ,  $Ype$ ,  $Ope$ ) were averaged for each individual  $i$  from birth to capture. Interaction between temperature and each biological covariate accounted for the thermal dependence of food conversion efficiency and predator-prey overlap, and generated a drop of model AIC (Akaike's

Information Criterion) compared to a simple additive formulation. The  $Y_c \times P$  interaction accounted for the effects of directional selection on mean growth rate (Edeline2007#1611).

We modeled temporal changes in the variance of  $\approx_{ij}$  with two different variance functions.

First, we modeled the residual variance ratio between  $P1$  and  $P2$

:

$$\text{var}[\approx_{ij}] = a \times \neq P \quad \text{Eq.6,}$$

where  $a$  is within  $Y_c$ , within  $S$ , within  $Bas$  residual variance during  $P1$  and  $\neq$  is the estimated ratio parameter. Second, we modeled changes in the variance of  $\approx_{ij}$  as a power function of  $Y_c$  inside each  $P$ , while accounting for the variance ratio between  $P1$  and  $P2$ :

$$\text{var}[\approx_{ij}] = b \times \neq' P^{\equiv \#P} \times Y_c \quad \text{Eq.7,}$$

where  $b$  is within  $Y_c$ , within  $S$ , within  $Bas$  residual variance in year-class 1944 (i.e., for the first  $Y_c$  of  $P1$ ),  $\neq'$  is the estimated variance ratio between the first  $Y_c$  of  $P1$  and the first  $Y_c$  of  $P2$ , and  $\equiv$  is the estimated within- $P$  power parameter. Eq.7 yielded a significantly better fit of  $\approx_{ij}$  in Eq.5 than Eq.6 ( $p < 0.05$ ). We modeled temporal changes in variance for natural log-transformed length-at-age-1 to age-6 using 6 age-specific linear REML mixed-effects models of the form:

$$\ln L_{ik} = \div_0 \div_1 S_i \div_2 Bas_i \div_3 T_i \div_4 Yp_i \div_5 Opi_i \div_6 Ype_i \div_7 Ope_i \div_8 Yc_i \times P_i b_k \approx_{ik} \quad \text{Eq.8,}$$

where  $\ln(L_{ik})$  is natural log-transformed body length-at-age  $x$  of individual  $i$  in group  $k$ ,  $\beta_{ij}$  are model coefficients, and  $\epsilon_{ij}$  represents normally distributed within-group residuals. Environmental growth conditions ( $T, Y_{pi}, O_{pi}, Y_{pe}, O_{pe}$ ) were averaged from birth to age  $x$ . This simpler formulation of fixed effects (compared to Eq.5) yielded a lower AIC for the majority of ages and was thus retained for all ages for parsimony and consistency. Each model had a different structure of normally distributed random effect  $b_k$ , which was selected among a set of candidate structures based on model AIC (details provided in Table 2). We modeled changes in the variance of  $\epsilon_{ik}$  in Eq.8 with Eq.6 and Eq.7, which yielded a significantly better model fit than Eq.6 ( $p < 0.05$ ) for all lengths-at-age except for length-at-age-2.

Finally, estimated parameters  $\beta_{ij}$ ,  $\beta'_{ij}$  and  $\beta_{ijk}$  from Eq. 6 and Eq.7 inserted in the above-listed models allowed us to quantify percent changes in residuals phenotypic variance for each trait (lifetime somatic growth and 6 lengths-at-age, Table 3). For instance, for  $g_i$ ,  $\beta_{ij} = -0.96$  in Eq.6 indicating that residual variance for  $g_i$  overall decreased by 4% between  $P1$  and  $P2$ . In Eq.7,  $\beta'_{ij} = 1.41$ ,  $\beta_{ijk} = 0.01$  during  $P1$  (19 year-classes), and  $\beta_{ijk} = -0.1$  during  $P2$  (30 year-classes), indicating that residual variance in  $g_i$  increased by 3.8% during  $P1$  and decreased by 29.6% during  $P2$  (see Table 3 for full results).

## RESULTS

### Raw trends in pike phenotypic variance

Raw variance in individual pike lifetime somatic growth rate among sampled fish increased up to the early 1960s (figure 1c, top panel), in accordance with the prediction that disruptive fishery selection on body size simultaneously favoured both slow and fast growers.

Directional fishery selection for slow growth and delayed entry to the fishery is self evident

and has already been demonstrated (Carlson2007#1537)(Edeline2007#1611). However, concurrent selection for fast growth is less intuitive. Therefore, we inspected fishery survival probability as a function of somatic growth rate in pike larger than 54 cm body-length, i.e., pike already recruited into the fishery (see Materials and Methods). Once recruited into the fishery, faster growers had increased survival probability (figure 1*b*;  $n = 15,972$ ;  $p < 0.001$ ), confirming that the fishery was disruptive not only on pike body size, but also on pike somatic growth rate. After the early 1960s, sampled pike had a decreased variance in somatic growth (figure 1*d*, top panel), in accordance with the prediction that stabilizing natural selection on body size selected against both slow and fast growers.

Raw trends in somatic growth rate were transmitted into corresponding trends in length-at-age. Variance in length-at-age-3 and age-4 (the two age-classes most strongly affected by the fishery, see Table 1) increased at the start of the time series and decreased at its end (figure 1*c*, down panel). However, the intensity of disruptive fishery selection was not strong enough to generate bimodality in length-at-age distributions (figure 3), probably due to weak fishing mortality (see introduction). Temporal fluctuations in somatic growth rate and length-at-age-3 and age-4 were statistically significant when tested with generalized additive models in which natural log-transformed variance was the response and a smoothed *Year class* term was the predictor (somatic growth rate:  $n=49$ ;  $p < 0.001$ ; length-at-age-3 and age-4:  $n=98$ ;  $p < 0.001$ ). Taken together, raw trends are remarkably consistent with the prediction that disruptive fishery selection opposed the effects of stabilizing natural selection in increasing pike phenotypic variance. As a second step of our analysis, we applied analytical methods aiming at testing for a possible sampling bias and at removing environmental noise into raw trends.

## Modeled trends in pike phenotypic variance

The reconstructed unbiased trend in somatic growth variance (figure 1d) is in close agreement with the trend observed in raw data (i.e., variance increased up to the early 1960s and decreased afterwards), indicating that patterns observed in the raw data reflect true patterns that occurred in the population. After having validated that our data were not biased, we accounted for environmental noise into pike phenotypic variance using statistical models in which we explicitly modeled temporal changes in residual variance (see Materials and Methods). Results are shown in Table 3 (statistical significance is considered when both confidence limits have the same sign). Residual variance significantly decreased for *all* analyzed traits from *Period 1* of dominating fishery selection (year classes from 1944 to 1963) to *Period 2* of dominating natural selection (year classes from 1964 to 1993). Moreover, across *Period 1*, residual variance increased in *all* traits, although statistical significance was not reached for somatic growth rate, length-at-age-1 and length-at-age-6 (Table 3). Residual variance in length-at-age-1 and length-at-age-2 increased despite the fact that age-1 pike were not caught by the fishery and that nonlinear fishery selection was not statistically significant on age-2 pike (Table 1), a result reflecting disruptive fishery selection on lifetime somatic growth rate. Interestingly, residual variance in length-at-age-3 to age-6 pike increased in parallel with the amplitude of nonlinear fishery selection gradients acting on these age-classes (Table 1), further supporting the view that the fishery was the primary driver of increased pike phenotypic variance across *Period 1*. Across *Period 2* of dominating natural selection, natural selection became increasingly stabilizing and fishery selection tended to be less disruptive (figure 1a). In parallel, variance in body length decreased significantly in all analyzed traits except length-at-age-2 (Table 3). Lack of change in variance for length-at-age-2 might be linked to exceptionally weak stabilizing natural selection combined with relaxation

of strongly directional fishery selection on this age class (Table 1). To sum up, our results support the view that pike phenotypic variance tracked the curvature of the adaptive landscape, which was imposed by the dominating selective force.

## **Discussion**

Our results empirically demonstrate that the common *a priori* assumption that harvesting causes size truncation and decreased trait variability may be wrong. In Windermere, gillnet fishing instead caused disruptive selection and increased trait variability. Therefore, careful consideration of the exact form of selection should precede inference about the mechanisms through which populations are negatively affected by harvesting. Our field-based findings are consistent with laboratory-based experiments in fruit flies *Drosophila melanogaster* and mice *Mus musculus* demonstrating that disruptive selection increases genetic variability and capacity to respond to selection (Roff1997). Accordingly, in Windermere pike a fishery-driven increase in capacity to respond to selection might have favoured the observed rapid evolutionary rebound after relaxation of the fishing pressure (Edeline2007#1611) (Conover2007)(Coltman2008). Interestingly, stabilizing natural selection decreased Windermere pike trait variance as observed in other systems (Roff1997)(Haugen2008), and disruptive fishery selection might thus have paradoxically increased pike capacity to respond to selection compared to a pristine pike population.

In contrast to Windermere pike, several fish stocks have been found to be unable to rebound after relaxation of fishing (Berkeley2004)(Hutchings2008)(Hutchings2000) (Sinclair2002#1148). For instance, cod in the southern Gulf of St. Lawrence collapsed in the early 1990s and has still failed to recover since the fishery was closed in 1993 (Sinclair2002#1148). To our knowledge, the southern Gulf of St. Lawrence cod is the only

population beside Windermere pike for which the exact form of fishery selection has been investigated. Fishery selection acting on cod body size changed from disruptive in the 1970s to truncation selection in the 1980s and early 1990s (i.e., before and during stock collapse), indicating that disruptive fishing can also occur at commercial exploitation rates. The change in the form of fishery selection was due to a parallel increase in both the fishing effort (that reduced survival in medium-sized cod) and in the minimum mesh-size of fishing gears (that reduced survival in large cod) (Sinclair2002#1148). Increasing minimum size limits is generally intended as a conservative measure allowing intensification of exploitation rates, but it might instead favor erosion of genetic variance for somatic growth and correlated traits, promote population collapse, and impair recovery. In contrast, maintaining disruptive harvesting necessitates combining slot size regulations (to preserve large individuals) with moderate exploitation rates (so that enough medium-sized individuals survive to a large size). Therefore, managed disruptive harvesting might represent a comprehensive and efficient tool for sustainable exploitation of living resources.

**Acknowledgments.** We are grateful to the many individuals who have participated in the Windermere data collection over the years. We also thank the Freshwater Biological Association for their joint stewardship of these invaluable data. We thank Leif Chr. Stige (CEES) for invaluable advice concerning variance functions in mixed-effects models. Thomas F. Hansen (CEES) provided helpful suggestions at an early stage of the study. We thank Stephanie M. Carlson (University of California, Berkeley) for commenting on our manuscript. E.E. received support from the Research Council of Norway and A.L.R. received support

from a Marie Curie Post Doc fellowship. Support from the Natural Environment Research Council to the Centre for Ecology & Hydrology is also acknowledged.

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**Table 1.** Directional (linear) and nonlinear selection gradients acting on Windermere pike body size from age-1 to age-6.

Positive directional gradients indicate that large fish were favoured, while negative directional gradients indicate that small fish were favoured. Positive nonlinear gradients indicate disruptive selection (i.e., that intermediate-sized fish had the lowest survival probability), while negative nonlinear gradients indicate stabilizing selection (i.e., that intermediate-sized fish had the highest survival probability).

Phenotypic trait	FISHERY SELECTION						N	NATURAL SELECTION						N
	Directional (linear) gradients			Nonlinear gradients				Directional (linear) gradients			Nonlinear gradients			
	Coefficient	SE	P-value	Coefficient*	SE*	P-value		Coefficient	SE	P-value	Coefficient*	SE*	P-value	
<b>Length-at-age-1</b>								0.47	0.15	0.0019	-0.22	0.30	0.4597	443
<b>Length-at-age-2</b>	-1.27	0.17	<0.0001	-0.12	0.25	0.6183	13942	0.72	0.04	<0.0001	-0.06	0.06	0.3514	4331
<b>Length-at-age-3</b>	-1.75	0.04	<0.0001	1.33	0.10	<0.0001	13898	0.68	0.03	<0.0001	-0.40	0.06	<0.0001	4870
<b>Length-at-age-4</b>	-0.77	0.02	<0.0001	1.21	0.05	<0.0001	11584	0.59	0.03	<0.0001	-0.41	0.05	<0.0001	4497
<b>Length-at-age-5</b>	-0.20	0.03	<0.0001	0.76	0.05	<0.0001	6316	0.45	0.04	<0.0001	-0.38	0.05	<0.0001	3830
<b>Length-at-age-6</b>	0.03	0.04	0.3979	0.42	0.07	<0.0001	2822	0.29	0.04	<0.0001	-0.32	0.05	<0.0001	3155

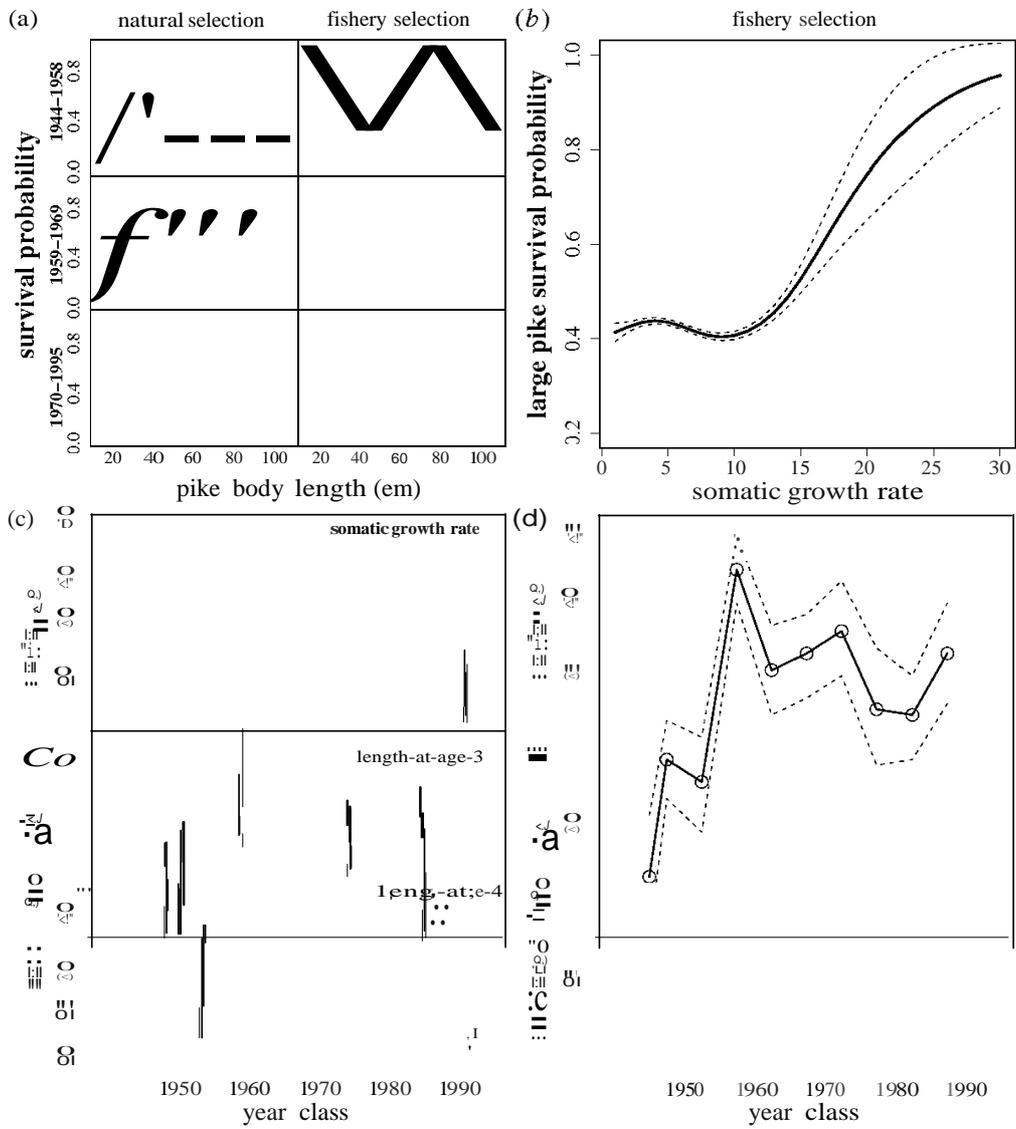
\*: Calculated by doubling regression coefficients (Stinchcombe2008)

**Table 2.** Details of the random effects structure for each linear REML mixed effects model used to estimate changes in Windermere pike residual phenotypic variance.

Response	Random effects, model parameters allowed to vary randomly	Number of groups N, number of observations n	Variance-covariance matrix for the random effects
Lifetime somatic growth	<i>Year class</i> nested into <i>Sex</i> , nested into <i>Basin</i> , random intercept	N=197, n=13942	Identity
	Age-1 <i>Year class</i> nested into <i>Basin</i> , random intercept	N=99, n=13941	Identity
	Age-2 <i>Year class</i> nested into <i>Basin</i> , random intercept	N=99, n=13941	Identity
	Age-3 <i>Year class</i> , random intercept and random <i>Sex*Basin</i> effect	N=50, n=13898	Symmetric
Ln (Body length)	Age-4 <i>Year class</i> nested into <i>Sex</i> nested into <i>Basin</i> , random intercept	N=196, n=11584	Identity
	Age-5 <i>Year class</i> , random intercept and random <i>Sex*Basin</i> effect	N=48, n=6316	Symmetric
	Age-6 <i>Year class</i> , random intercept and random <i>Basin</i> effect	N=47, n=2822	Symmetric

**Table 3.** Estimated percent changes in Windermere pike residual phenotypic variance with respect to periods of dominating fishery selection (*P1*) and dominating natural selection (*P2*).

Phenotypic trait	Change in variance from <i>P1</i> to <i>P2</i> (in % with 95% C.I.)	Change in variance within <i>P1</i> (in % with 95% C.I.)	Change in variance within <i>P2</i> (in % with 95% C.I.)
Lifetime somatic growth rate	-4.0 (-6.5, -1.5)	+3.8 (-3.4, +11.5)	-29.6 (-44.0, -11.5)
Length-at-age-1	-9.5 (-11.7, -7.4)	+3.2 (-3.9, +10.8)	-28.1 (-44.2, -7.4)
Length-at-age-2	-11.5 (-13.5, -9.3)	+21.2 (+11.2, +32.0)	+2.7 (-3.9, +9.8)
Length-at-age-3	-7.0 (-9.2, -4.8)	+53.6 (+40.0, +68.4)	-33.9 (-47.4, -17.0)
Length-at-age-4	-5.8 (-8.2, -3.3)	+48.2 (+33.0, +65.2)	-45.5 (-58.2, -29.0)
Length-at-age-5	-6.4 (-9.7, -3.0)	+21.2 (+3.6, +41.7)	-48.1 (-64.1, -24.9)
Length-at-age-6	-8.0 (-12.8, -2.9)	+0.59 (-25.1, +35.0)	-52.6 (-74.8, -10.5)



**Figure 1.**

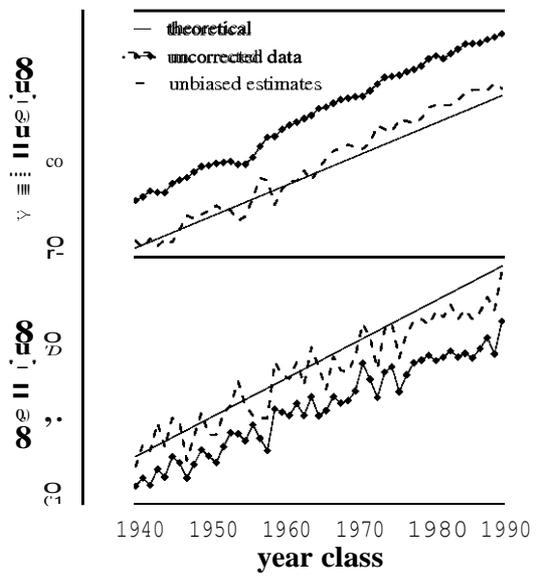
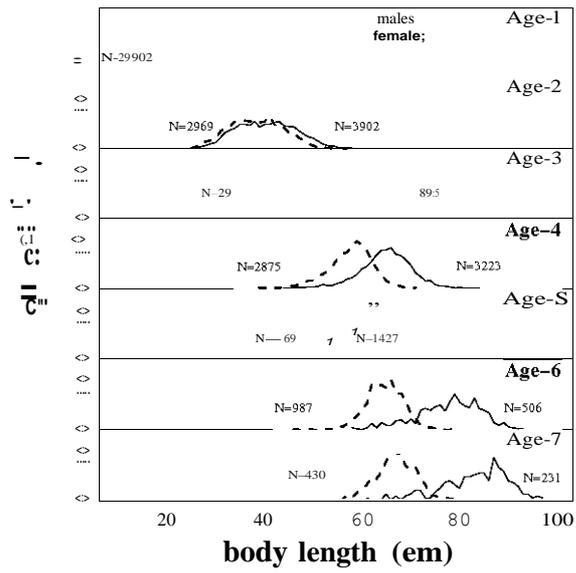


Figure 2.



**Figure 3.**

## Figure Legends

**Figure 1.** Context for selection in Windermere pike (*Esox lucius*) and associated temporal changes in pike phenotypic variance. (a) Nonlinear relationship between pike body length and an individual's survival probability through natural selection and fishery selection, separated into 3 time periods covering the entire time series. **Note that natural selection tended to be increasingly stabilizing over time while fishery selection tended to be less disruptive.** (b) Nonlinear relationship between large pike (55 cm body length and longer) somatic growth rate ( $\text{cm year}^{-1}$ ) and an individual's survival probability through fishery selection with 95% confidence intervals. (c) Observed time series of natural log-transformed variance for lifetime somatic growth rate (von Bertalanffy asymptotic length) and length-at-age-3 and age-4 (both in cm, y axis on a log scale). Bold dashed line is a smoother of the effect of year class. (d) Unbiased change in phenotypic variance with 95% confidence intervals for pike lifetime somatic growth rate (von Bertalanffy asymptotic length in cm, data pooled by groups of 5 year classes, y axis on a log scale).

**Figure 2.** Model validation for maximum likelihood estimation of unbiased phenotypic variances (top panel) and means (down panel) in Windermere pike.

**Figure 3.** Sex-specific distributions of backcalculated length-at-age-1 to age-7 of Windermere pike born between 1944 and 1963 (period of dominating fishery selection) showing absence of bimodality. Numbers on the left of the curves indicate male sample size and numbers on the right of the curves indicate female sample size.