Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection

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1   **Selective harvest of large individuals should alter natural adaptive landscapes and**

2   **drive evolution towards reduced somatic growth and increased reproductive**

3   **investment. However, few studies have simultaneously considered the relative**

4   **importance of artificial and natural selections in driving trait changes in wild**

5   **populations. Using 50 years of individual-based data on Windermere pike (*Esox***

6   ***lucius*), we show that trait changes tracked the adaptive peak, which moved in the**

7   **direction imposed by the dominating selective force. Individual lifetime somatic**

8   **growth decreased at the start of the time series because harvest selection was**

9   **strong and natural selection was too weak to override the strength of harvest**

10   **selection. However, natural selection favoring fast somatic growth strengthened**

11   **across the time series in parallel with the increase in pike abundance and,**

12   **presumably, cannibalism. Harvest selection was overridden by natural selection**

13   **when the fishing effort dwindled, triggering a rapid increase in pike somatic**

14   **growth. The two selective forces appear to have acted in concert during only one**

15   **short period of prey collapse that favored slow-growing pike. Moreover, increased**

16   **somatic growth occurred concurrently with a reduction in reproductive investment**

17   **in young and small female pike, indicating a trade-off between growth and**

18   **reproduction. The age-specific amplitude of this change paralleled the age-specific**

19   **strength of harvest pressure, suggesting that reduced investment was also a**

20   **response to increased life expectancy. This is the first study to demonstrate that a**

21   **consideration of both natural selection and artificial selection is needed to fully**

22   **explain time-varying trait dynamics in harvested populations.**

23 Selective harvest of the largest individuals may add a strong and temporally consistent

24 directional component to the natural selective forces shaping adaptive landscapes (1).

25 Theory predicts that such consistent selection should induce life history evolution (2-4).

26 Accordingly, recent studies in nature indicate a correlation between increased harvest

27 pressure and phenotypic changes in plants (5) and vertebrates (6). Harvest-induced

28 phenotypic changes have been studied extensively in fisheries, where harvest is often

29 associated with decreased somatic growth and/or decreased age and size at maturity (7-

30 9). Under laboratory conditions, artificial selection against large size has been shown to

31 induce rapid evolution towards slower growth (10), and to promote genetically-based

32 reductions in fecundity, larval viability, and foraging efficiency (11). These harvest-

33 induced changes are generally considered maladaptive (11), because harvest and natural

34 selection can act in different directions (1). However, to date, no study has examined the

35 relative contributions of harvest and natural selection in driving trait changes in wild,

36 harvested populations. We performed this task in pike (*Esox lucius*) from Windermere

37 (UK). This system is particularly well-suited for this endeavor because we have

38 previously demonstrated that natural and fishery selection act in opposite directions on

39 Windermere pike body size (1).

40   Windermere is a glacial valley lake divided by shallows into two basins of

41 different productivity and constituting different habitats for pike (12, 13) (Fig. 1A).

42 Commercial net fisheries for several species including pike have operated on

43 Windermere since the 12th century but were terminated in 1921 due to heavy fishing

44 problems (13). Le Cren (13) suggested that, by 1939, the fish population of Windermere

45 consisted mainly of a dense population of perch (*Perca fluviatilis*) and a moderate

46 population of pike feeding mostly on perch and, to a lesser degree, charr (*Salvelinus*

47 *alpinus*) and trout (*Salmo trutta*). Gillnet fishing for pike was initiated in 1944 with two

objectives: (i) increase the density of perch (by far the most abundant prey item in pike

diets (14)), which were used as human food during wartime and (ii) to provide

information that would illuminate the overfishing problem (13). The fishing methods

for pike and gear used (64 mm mesh size gill-nets) remained constant until the present

time, but the exploitation rate decreased overall to reach a very low level after 1980

(Fig. 1C). The scientific fishery is the only removal fishery for pike and targets

individuals longer than 55 cm (15), although recent evidence suggests that the largest

pike are less susceptible to capture (1). Male and female pike typically mature at age 2

(i.e., before recruitment to the fishery which occurs mainly at age 3 for females and 4

for males (15)). Captured pike are measured for body length (cm, measured as fork

length), weighed (kg), sexed, and opercular bones are removed for age and length back-

calculation following a method validated for Windermere pike by Frost and Kipling

(16). Bone density differs between summer and winter, producing narrow bands

(hereafter "check") that are deposited on the opercular bones during slow winter

growth. These checks then serve as an annual mark and, thus, allow the aging of

individual fish. 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

(16). In the present work, the growth data therefore represent length-at-age data

collected on individual pike from age-1 to age-at-capture. In addition to growth data,

data on female reproductive investment (gonad-weight, egg-number and egg-weight,

which is a proxy for egg-size) were collected since 1963 (15), which coincides with the

time that the exploitation rate dropped (Fig. 1C). Together with these biological data,

surface water temperatures were recorded on a near daily basis and were here averaged

for each year. Finally, the abundance of pike and perch have been estimated annually

72   for the 1944-1995 period, separately for each basin as well as separately for young (age

73   = 2) and old individuals (age > 2) (17).

74   Natural and harvest selection have been previously quantified for the

75   Windermere pike population through an estimation of the strength, direction, and form

76   (directional, nonlinear) of the two selective forces (1). This earlier work demonstrated

77   that harvest and natural selection often acted in opposite directions on pike body length

78   (1). In particular, directional natural selection tended to favor long pike whereas the

79   fishery targeted long individuals. Moreover, nonlinear natural selection tended to be

80   stabilizing in Windermere, favoring pike of intermediate lengths, whereas fishery

81   selection tended to be disruptive, favoring short and long pike (1). Large pike

82   presumably have an advantage over small pike in terms of natural selection in that they

83   are not susceptible to cannibalism, which can be severe in pike (18). Moreover, large

84   pike likely have an advantage in terms of intrasexual combat for females during the

85   breeding season (18).

86   The context for selection in Windermere changed across the five decades of

87   study. From 1944 to 1995, pike numbers increased while perch numbers declined over

88   the same period (Fig. 1B), likely resulting in increased agonistic interactions and

89   cannibalism within the pike population. Consistent with this view, selection analyses

90   indicate that stabilizing selection acting on Windermere pike body length overall

91   strengthened through time (1) (i.e., that natural selection favoring fast somatic growth to

92   reach the optimum length has increased). However, natural selection often fluctuates in

93   connection with severe environmental variations (19). In Windermere, collapse of the

94   perch population due to a disease outbreak in 1976 (20) was likely the most severe

95   environmental disturbance experienced by pike across the entire time series (Fig. 1B).

96   Severe food stresses have been shown to select against fast growth (21). Therefore,

97   ignoring fishery selection, we hypothesized that natural selection would drive an

98   increase in pike somatic growth across the study period, except when the perch

99   population collapsed in 1976. However, we also expected the fishery to simultaneously

100   operate in the opposite direction and consistently drive decreased growth, but with a

101   lesser effect when fishing intensity was reduced. Finally, if natural selection drove

102   evolutionary change towards faster somatic growth, we would also expect a concurrent

103   reduction in reproductive investment due to the trade-off between growth and

104   reproduction (2, 3).

105   To test these hypotheses in a robust framework, we used mixed-effects models

106   ((22), see also Materials and methods for an extensive description of our models). In

107   these models we have taken into account the many possible environmental variables

108   (i.e., basin productivity, water temperature, pike numbers, and prey density) known to

109   plastically affect somatic growth (e.g., increased abundance may reduce growth through

110   a density-dependent food limitation). Additionally, because reproductive decisions are

111   also functions of surplus energy gained prior to spawning (23), we have taken into

112   account the effect of somatic body condition (hereafter "fatness") in estimating changes

113   in individual reproductive investment (see Materials and methods). By considering the

114   potential effects of harvest selection and natural selection, we demonstrate that both

115   selective forces played a role in driving trait changes in Windermere pike across five

116   decades.

117

118   **Results**

119   We first tested for an overall change in pike somatic growth across the entire time series

120   by modeling the linear effect of time on individual lifetime growth (asymptotic length,

121   see Materials and methods). We found that pike somatic growth increased significantly

122   over the 1944-1995 period (Table 1). To evaluate shorter time-scale changes in relation

123   to periods of varying strengths of natural and fishery selection, we modeled nonlinear

124   changes in individual pike lifetime growth (Fig. 1D, see Materials and methods). The

125   nonlinear trend, shown in Fig. 1D, may be separated into 4 phases, which we describe

126   below.

127   During the first phase, from 1944 to the early 1960's, somatic growth slightly

128   decreased, suggesting that the selection imposed by fishing overwhelmed the strength of

129   natural selection. There was a remarkably close match between the peak of fishing

130   pressure in 1963 (Fig. 1C) and the slowest growth observed across the entire time series

131   in year classes born from 1960 to 1963 (Fig. 1D) (i.e., year classes for which both the

132   parents and the offspring experienced strong fishing pressure). During the second phase,

133   1963 to the mid-1970's, pike somatic growth increased rapidly, suggesting that natural

134   selection overwhelmed fishery selection during this time period (Fig. 1D). Pike somatic

135   growth stabilized in fish born in the early 1970's, suggesting that phenotypic adjustment

136   to the new adaptive peak took approximately 10 years, a delay corresponding to 2 to 5

137   pike generations (i.e., Windermere pike first reproduce at age 2 but the mean generation

138   time, calculated as the mean age of mature females weighed by their gonad weight, was

139   estimated to be 5.2 years). During the third phase, from the mid-1970's through the mid-

140   1980's, pike somatic growth decreased slightly, most likely due to an inversion in the

141   direction of natural selection that then acted in concert with fishery selection. Indeed, in

142   1976 a disease outbreak induced a collapse of the perch population (20) while pike

143   numbers were relatively high (Fig. 1B). Food stress might have thus induced starvation

144   that ultimately selected against fast growth (21). The perch collapse was followed by a

145   sharp decrease in pike numbers (Fig. 1B), supporting the view that prey shortage

146   induced selection in the pike population through severe starvation. During the fourth

147   phase, from the mid-1980's to the mid-1990's, pike somatic growth increased very

148   rapidly, a period corresponding to the highest pike numbers of the time series, the

149   lowest fishing pressure, and relatively low and fluctuating perch densities (Figs. 1B and

150   1C).

151   Overall, this nonlinear trend confirms that fishery and natural selection were

152   operating simultaneously in opposite directions (1) and also supports the prediction that

153   pike somatic growth variation responded to the dominant selective force. Fishery

154   selection was overwhelmed by natural selection during the early 1960's (leading to the

155   change from phase 1 to phase 2). Additionally, females grew faster than males overall,

156   and increased their growth rates at a faster rate than males over the study period (Table

157   1). This later result indicates that, as faster growers, females experienced stronger

158   fishery selection than males, and thus benefited more from the relaxation in the fishing

159   pressure later in the time series. Finally, pike grew significantly faster in the more

160   productive south basin compared to the less productive north basin (Table 1).

161   Concurrent with the increase in somatic growth after the early 1960's, we found

162   that young – but not old – female pike reduced their reproductive investment (Fig. 2,

163   Table 1), providing support for our third hypothesis of a trade-off between growth and

164   reproduction in Windermere pike. Indeed, the age-specific intercept of the reproductive

165   investment/length reaction norm decreased significantly for gonad-weight and egg-

166   number, but not egg-weight (Fig. 2, *Year* effect in Table 1). Egg-weight is positively

167   correlated to offspring size, and competition is predicted to favor large egg-size (3).

168   Hence, maintenance of egg-weight despite decreased investment suggests increased

169   competition in young pike in connection with increased pike density. At the same time,

170   the age-specific slope of the investment/length reaction norm increased, indicating that

171   female pike were investing in reproduction at a larger size (Fig. 2). This increase in the

172 *Length*Year* interaction was statistically significant for gonad-weight and egg-number

173 but not egg-weight (Table 1). In contrast, at any given length, the age at which

174 investment occurred (*Age*Year* interaction) increased significantly for egg-weight only

175 (Table 1). Finally, the magnitude of the aforementioned changes in investment

176 decreased significantly with the age for both gonad-weight and egg-weight (Fig. 2,

177 *Length*Year*Age* interaction in Table 1). In order to determine whether this

178 *Length*Year*Age* effect was related to age-specific differences in the relaxation of

179 fishery selection after the early 1960's, we calculated age-specific mean fishery

180 selection differentials for females at each age (see Materials and methods). We found

181 that fishery selection decreased with increasing age, and was substantial on age 3

182 females only (Fig. 2), supporting the view that reduced reproductive investment was not

183 only a response to strengthening natural selection but also related to increased life

184 expectancy. Finally, somatic body condition had a positive effect on investment

185 (significant on gonad-weight and egg-number, Table 1), confirming that surplus energy

186 gained prior to reproduction plastically affects energy allocation to reproduction (23).

187

188 **Discussion**

189 Wild populations are continually subject to natural selection, which temporally

190 fluctuates in direction and/or magnitude (19). Natural selection acting on Windermere

191 pike is presumably a function of both conspecific and prey (perch) densities. Prior to

192 1944, pike abundance was relatively low while perch were abundant (13), presumably

193 creating conditions for weak competition for food and low cannibalism (i.e., weak

194 natural selection for fast growth). However, throughout most of the time series under

195 consideration, pike abundance was increasing while perch abundance was decreasing.

196 These conditions set the stage for selection favoring fast growth presumably through

197   cannibalism, because encounter rates between pike were increasing while prey

198   abundance remained high enough to support fast growth in pike. However, the perch

199   collapse in the mid-1970's seemed to reverse this trend during a short period by

200   selecting for slow growth. This result provides support for previous work which

201   suggested that nutrient stress is a strong agent of selection against fast somatic growth

202   in both plants and animals (21). Together, these results suggest that the fitness of fast

203   growing pike as a function of the pike/perch ratio is dome-shaped in Windermere (i.e.,

204   for a pike, relatively large size confers fitness advantages as long as prey abundance is

205   not too low). Cannibalism is generally considered as a "life-boat" mechanism allowing

206   populations to survive under decreased food conditions (24). Our results lead us to

207   modify this point of view by also suggesting that cannibalism can result in growth costs,

208   which may be detrimental under very severe food stress.

209   The fishery for pike in Windermere consistently selected against fast growth, but

210   the strength of this artificial selective force decreased across the time series. From the

211   early 1940's to the early 1960's (phase 1), fishery selection was strong enough to

212   override natural selection. The result was that combined selection favored decreased

213   somatic growth during this time period. During phase 2 (~10 years), relaxed fishing

214   pressure allowed natural selection to prevail and resulted in combined selection favoring

215   increased somatic growth. Phenotypic adjustment to the new adaptive optimum was

216   remarkably fast (2 to 5 generations). This result suggests that two slightly different

217   evolutionary processes were at work. Average heritability for growth in fish (h^2=0.3) is

218   high enough to cause substantial evolution in a few generations (25). However, due to

219   the very detailed data used here we probably also observed direct effects of the fishery

220   (i.e., direct removal of fast growing genotypes). Indeed, the slowest growth occurred in

221   year classes that immediately preceded the peak of fishing pressure (i.e., in year classes

222 that were born from parents that were strongly fished and that were themselves strongly

223 fished). Consequently, relaxed fishing pressure immediately increased the proportion of

224 fast growing genotypes in the population. Interestingly, Carlson et al. (1) did not

225 observe any significant change in the strength of directional selection acting on

226 Windermere pike (i.e., selection pushing the population towards the newly emerging

227 adaptive peak). They suggested that this was possibly due to the fact that pike quickly

228 attained equilibrium after fishing effort dwindled (1). Our results provide support for

229 their assertion.

230 We show that a rapid shift towards fast growth following decreased fishing

231 pressure was accompanied by a reduction in reproductive investment in young and

232 small females. This result strongly supports the prediction of a genetic trade-off

233 between growth and reproduction in Windermere pike (2, 3). Importantly, we have

234 accounted for the plastic effect of short-term variations in growth conditions in our

235 reaction norm approach. Indeed, in teleosts plasticity in reproductive decisions is

236 affected by the rate of surplus energy gained during critical periods (23). In Windermere

237 pike, energy used for reproduction in March and April is gained during the previous

238 summer (15). We have here estimated surplus energy gained during previous summer as

239 the somatic body condition (fatness) at capture, and we show that condition had a

240 positive effect on investment. After accounting for this plastic effect, we found that

241 investment at each reproduction decreased while the length at which investment

242 occurred increased. We further show that the age-specific amplitude of this later change

243 paralleled with the age-specific strength of fishing selection, suggesting that investment

244 change was partly a response to relaxation in the fishing pressure. Hence, our results

245 provide further support for previous research, which suggested that fisheries may induce

246 genetic change in the energy allocation rules to growth and reproduction in fish

247 populations (2, 4). Instead of investing in gonads early in life and at a small size due to

248 fishery-induced mortality, Windermere female pike now grow first to increase fitness

249 through the achievement of a larger size.

250 Our data suggest that up-to-1963 exploitation rates of 1.1 to 7.3 % (mean = 3.3

251 %) were enough to impede the effects of natural selection in Windermere pike and even

252 cause detectable evolution in the opposite direction. It is thus highly probable that

253 commercial harvest, that may deplete 45 to 99 % of the reproductive biomass (26), may

254 cause rapid evolution in commercial fish stocks. Temporal consistency of harvest

255 practices (e.g., systematic removal of the largest individuals) likely magnifies the

256 evolutionary impacts of exploitation. Introducing variety in harvest practices could limit

257 the amplitude of harvest-induced trait changes. However, our results point out that

258 knowing the intensity and direction of artificial selection is not always enough to predict

259 the response of populations to harvest. Instead, trait changes result from the combined

260 forces of both the harvest and natural selection, and evolution of harvested populations

261 is thus a process more complex than generally portrayed. Conservation plans that ignore

262 this complexity could lead to improper management decisions.

263

264 **Materials and methods**

265 **<u>Growth modeling</u>**

266 We have tested for linear change in growth during the 1944-1995 period using a

267 nonlinear mixed-effects model (random grouping factor n = 13,942 individuals, n =

268 65,123 observations). This model was based on the von Bertalanffy growth curve

269 (hereafter "VBGC", fitted to length-at-age data for each individual) and allowed us to

270 quantify the temporal trend in individual asymptotic length. Asymptotic length is an

271 index of lifetime somatic growth rate. The index thus synthesizes an individual's

272 decisions for energy allocation, and is particularly powerful to study life-history

273 variation and evolution. The trend in asymptotic length was estimated while

274 simultaneously controlling for the effect of basin productivity, and the effects of yearly

275 variations in water temperature, prey numbers, and pike density. Individual pike growth

276 was modeled with a 3 parameter formulation of the VBGC (27): $L(A)=\alpha+(\beta-\alpha)\gamma^A$, where

277 L=length (in cm), A=age, β=intercept, γ=rate of increase, and α=asymptotic length. This

278 formulation of the VBGC yielded the lowest Akaike's Information Criterion (AIC) and

279 less structure in the residuals compared with 6 other formulations of the VBGC and 8

280 other nonlinear models (the Gompertz, 3 and 4 parameters logistic, Pauly's, Morgan,

281 Mercer and Flodin, Weibul, modified Freundlich, Chapman-Richards, and Michaelis-

282 Menten models (27)). The selected VBGC equation was incorporated into a restricted

283 maximum likelihood (REML) nonlinear mixed-effects model (22) (nlme library of R

284 (28)):

285

286 $$L_{ij}=\alpha_{ij}+(B-\alpha_{ij})\gamma^{A_{ij}}+\varepsilon_{ij} \quad (\text{Eq. 1})$$

287

288 where L_{ij} is length of individual i in year j, ε_{ij} is a normally distributed within-individual

289 error term and the parameter α_{ij} is associated with fixed covariate effects and a random

290 individual effect:

291

292 $$\alpha_{ij}=\beta_0+\beta_1 T_j+\beta_2 Ypi_j+\beta_3 Opi_j+\beta_4 Ype_j+\beta_5 Ope_j+\beta_6 Bas_i+\beta_7 S_i+\beta_8 Y_i+\beta_9 T_j*Ypi_j+$$

293 $$\beta_{10}T_j*Opi_j+\beta_{11}T_j*Ype_j+\beta_{12}T_j*Ope_j+\beta_{13}Y_j*S_i+b_i \qquad (\text{Eq. 2})$$

294

295 where βs=model coefficients for the fixed-effects part where *Y=Year*, *S=Sex*,

296 *Bas=Basin*, *T=Temperature*, *Ypi=Young pike (age=2)*, *Opi=Old pike(age>2)*,

297   *Ype=Young perch (age=2), Ope=Old perch (age>2)*, and b_i is a normally distributed

298   random individual effect. Interaction between temperature and each biological covariate

299   accounted for the thermal dependence of food conversion efficiency and predator-prey

300   overlap, and generated very significant improvement of model AIC compared to a

301   simple additive formulation. Estimate of the main effects of *Y* and S (Table 1) was

302   obtained from a model in which the *Y*S* interaction was omitted from (Eq. 2). Both

303   models incorporated within-individual temporal autocorrelation (autoregressive

304   function of time of order 1) and handled heteroscedasticity by modeling the variance of

305   ε_{ij} as the product of a sex-specific power function of *A* and a linear function of *Y*. Fig.

306   1D was obtained from a generalized additive mixed effects model (GAMM, mgcv

307   library of R (29)) in which individual asymptotic length (α_i) was the response

308   [computed from a model similar to (Eq. 1, Eq. 2) above, except that the fixed effects

309   part did not contain any covariate ($\alpha_i=\beta_0+b_i$ in (Eq. 2)], grouped by *S*, nested in *Bas*,

310   nested in *year class* (random grouping factor n = 197 groups, n = 13,942 individuals). In

311   the GAMM, predictors were as in (Eq.2) with no *Y*S* interaction, covariates were

312   averaged across individual life, and the linear *Y* effect was replaced by a nonlinear *year*

313   *class* effect (natural quadratic spline), thus removing any *a priori* expectation

314   concerning the shape of the trend.

315

316   **Reproductive investment modeling**

317   We have tested for temporal changes in the slope and intercept of the reproductive

318   investment/body length reaction norm of females born from 1963 to 1995 using linear

319   mixed-effects models including the full interaction between length, age, and time as

320   continuous variables (random grouping factor n = 41 years, n = 3,070 observations).

321   Rep_{ij} represents gonad-weight, egg-number (both ln-transformed), or egg-weight of

322   individual i in year j, and were modeled with REML linear mixed-effects models:

323

324   $Rep_{ij}=\beta_0+\beta_1 A_{ij}+(\beta_2+b1_j)\ln L_{ij}+\beta_3 Y_j+\beta_4 M_i+\beta_5 Kns_i+\beta_6 \ln L_{ij}*Y_j+\beta_7 A_{ij}*\ln L_{ij}+\beta_8 Y_j*A_{ij}+\beta_9 A_{ij}*\ln$

325   $$L_{ij}*Y_j+b2_j+\varepsilon_{ij} \quad (Eq.\ 3)$$

326

327   where βs=model coefficients for the fixed-effects part, $b1_j$ and $b2_j$ are normally

328   distributed random year-effects (with a symmetric covariance matrix), and ε_{ij} is a

329   normally distributed within-year error. Fixed-effect covariates were A=age, ln$L$=natural

330   log of length (in cm), Y=year (continuous variable), M=month of capture (from October

331   to February). *Kns* was the relative somatic condition factor (30): $Kns=100*SM/SM_{std}$,

332   where SM is the somatic mass (total mass-gonad mass) and SM_{std} is the predicted

333   somatic mass of a fish of the same length L, as calculated from the ln(SM)-ln(L)

334   regression equation (least squares mean fit, N=3,694; R^2=0.96). Somatic body condition

335   was found to have a higher effect on reproductive investment than previous growth

336   history (α and last growth increment) during model selection procedure based on AIC.

337   The M effect on egg-number was not significant and was thus omitted from egg-number

338   modeling. Estimates of the main effects of ln$L$, A and Y (Table 1), were obtained from a

339   model in which the interactions were omitted from (Eq. 3). The models handled

340   heteroscedasticity by modeling the variance of ε_{ij} as the product of exponential

341   functions of A and ln$L$. Predicted values in Fig. 2 were computed from the interaction

342   model. Finally, selection differentials provided in the reproductive investment analysis

343   and in Fig. 2 were estimated for each year and each age as the mean backcalculated

344   length of females that escaped the fishery (but were caught eventually) minus the mean

345 length of females of the same age caught into the fishery (9) for the entire study period

346 (1945-1995).

347

357

358 **Author contributions**. E.E. and S.M.C. conceived the study. E.E. and L.C.S.

359 performed the statistical analyses. E.E. wrote the paper in dialogue with all coauthors,

360 all of whom participated in the interpretation of the statistical results. I.J.W., J.M.F. and

361 J.B.J. contributed to the collection of data and made them all available to the present

362 study, and T.O.H. organized the data set.

363

364 **Author information**. The authors declare that they have no conflicts of interests.

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Figure legends

Fig. 1. Windermere background information and growth time series for pike (*Esox*

lucius). (**A**) Map showing the location of the study lake (surface area 14.8 km^2) in the

Lake District of north-west England, U.K., and the division of the lake into two basins.

The southern basin is morphologically different from and more productive than the

northern basin. (**B**) Population size of pike (purple) and perch (bold, blue) showing

increased numbers of the predator and decreased numbers of the main prey (log 10

scale). Dashed lines represent age 2 individuals (termed "young"), solid lines represent

age 3 and older individuals (termed "old"). (**C**) Exploitation rate for pike with trendline,

representing the proportion of pike caught in the fishery during the winter compared to

the number of pike in the lake the previous spring. (**D**) Nonlinear temporal trend in

individual pike growth with 95% confidence intervals taking into account the effects of

variations in growth conditions (see Materials and methods). Points represent the partial

residuals for the smooth term (i.e., the residuals that would be obtained by dropping the

term concerned from the model while leaving all other estimates fixed). **Fig. 2.** Changes

in the gonad weight/body length reaction norm of age-3 to age-8 female pike in

Windermere. Lines represent predicted values for 1963 (bold, red) and 2003 (blue) with

95% confidence intervals (dotted lines), and were estimated from data for the 1963 to

1995 year classes. *S* is the age-specific mean selection differential (in cm, ± SD) from

fishery selection on females from 1945 to 1995 (see Materials and methods). Decrease

in the intercept of the investment/body length reaction norm (*Year* effect in Table 1)

indicates decreased investment at any age and length. Concurrent increase in the slope

of the investment/body length reaction norm (*Length*Year* interaction in Table 1)

indicates that investment now occurs at a larger size. The magnitude of these changes

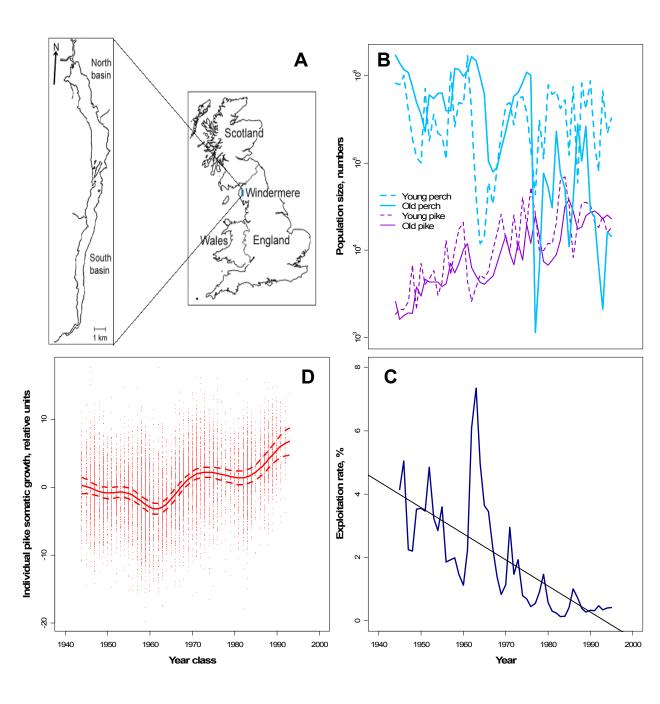was inversely proportional to the age (*Length*Year*Age* interaction in Table 1).
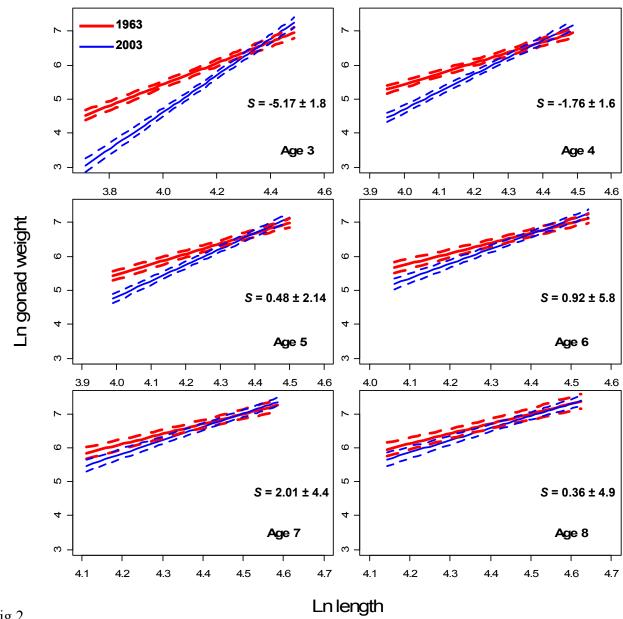
Fig. 1

Fig.2

Table 1. Parameter estimates and their statistical significance in the different mixed effects models used to model temporal changes in vital rates of Windermere pike.

Response	Random grouping factor	Fixed effects	Estimate	F-value (numerator df, denominator df)	p-value
Length at age	**Individual (13,942 levels)**	Temperature (degrees C)	3.80 e-1	2.95 e+3 (1, 51166)	<0.0001
		Young pike (numbers)	1.63 e-4	7.86 e+3 (1, 51166)	<0.0001
		Old pike (numbers)	1.08 e-4	3.14 e+2 (1, 51166)	<0.0001
		Young perch (numbers)	-4.00 e-6	2.60 e+3 (1, 51166)	<0.0001
		Old perch (numbers)	-7.46 e-6	6.55 e+3 (1, 51166)	<0.0001
		Basin (2 levels)	2.87 e-1	1.27 e+2 (1, 51166)	<0.0001
		Sex (females relative to males)	1.19 e+1	3.70 e+4 (1, 51167)	<0.0001
		Year (numbers)	1.58 e-1	1.65 e+5 (1, 51167)	<0.0001
		Temperature*Young pike	-1.33 e-5	1.61 e+3 (1, 51166)	<0.0001
		Temperature*Old pike	-1.60 e-6	7.80 e+3 (1, 51166)	<0.0001
		Temperature*Young perch	4.05 e-7	1.46 e+3 (1, 51166)	<0.0001
		Temperature*Old perch	7.14 e-7	2.12 e+3 (1, 51166)	<0.0001
		Sex*Year	2.01 e-1	2.79 e+3 (1, 51166)	<0.0001
ln Gonad weight	**Year (factor variable, 39 levels)**	Month	-2.20 e-2	9.38 e+1 (1, 3023)	<0.0001
		Kns (somatic body condition)	6.20 e-3	4.94 e+1 (1, 3023)	<0.0001
		ln Length (cm)	4.01	7.21 e+3 (1, 3027)	<0.0001
		Age (numbers)	-1.55 e-2	6.15 (1, 3027)	0.0132
		Year (numbers)	-6.79 e-3	1.59 e+1 (1, 37)	0.0003
		ln Length*Age	1.59 e+1	2.49 e+1 (1,3023)	<0.0001
		ln Length*Year	8.15 e-2	7.00 e+1 (1, 3023)	<0.0001
		Year*Age	3.46 e-2	1.64 (1, 3023)	0.2004
		ln Length*Year*Age	-8.10 e-3	9.30 (1, 3023)	0.0023
Egg weight	**Year (factor variable, 39 levels)**	Month	-8.38 e-5	3.74 e+2 (1,3023)	<0.0001
		Kns (somatic body condition)	3.20 e-6	2.20 (1, 3023)	0.1382
		ln Length (cm)	1.43 e-3	2.98 e+1 (1, 3027)	<0.0001
		Age (numbers)	-9.33 e-6	2.88 e-1 (1, 3027)	0.5915
		Year (numbers)	-4.97 e-6	1.29 (1, 37)	0.2627
		ln Length*Age	4.05 e-2	1.95 e-1 (1, 3023)	0.6592
		ln Length*Year	1.57 e-4	2.42 (1, 3023)	0.1196
		Year*Age	8.33 e-5	9.62 (1, 3023)	0.0019
		ln Length*Year*Age	-2.04 e-5	6.96 (1, 3023)	0.0084
ln Egg number	**Year (factor variable, 39 levels)**	Kns (somatic body condition)	4.96 e-3	4.75 e+1 (1, 3024)	<0.0001
		ln Length (cm)	3.56	3.62 e+3 (1, 3028)	<0.0001
		Age (numbers)	-1.34 e-2	8.80 (1, 3028)	0.0030
		Year (numbers)	-3.32 e-3	8.3 (1, 37)	0.0065
		ln Length*Age	4.14	4.58 e+1 (1, 3024)	<0.0001
		ln Length*Year	2.07 e-2	9.1 (1, 3024)	0.0026
		Year*Age	1.04 e-2	3.8 (1, 3024)	0.0513
		ln Length*Year*Age	-2.17 e-3	1.1 (1, 3024)	0.2965