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

Eric Edeline*, Stephanie M. Carlson*[†], Leif C. Stige*, Ian J. Winfield[‡], Janice M. Fletcher[‡], J. Ben James[‡], Thron O. Haugen*[§], L. Asbjørn Vøllestad*, and Nils C. Stenseth*[¶]

*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway; [†]School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195; [‡]Centre for Ecology and Hydrology, Lancaster Environment Centre, Bailrigg Avenue, Bailrigg, Lancaster, Lancashire LA1 4AP, United Kingdom; and [§]Norwegian Institute for Water Research, Gaustadalléen 21, 0349 Oslo, Norway

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Selective harvest of large individuals should alter natural adaptive landscapes and drive evolution toward reduced somatic growth and increased reproductive investment. However, few studies have simultaneously considered the relative importance of artificial and natural selection in driving trait changes in wild populations. Using 50 years of individual-based data on Windermere pike (*Esox lucius*), we show that trait changes tracked the adaptive peak, which moved in the direction imposed by the dominating selective force. Individual lifetime somatic growth decreased at the start of the time series because harvest selection was strong and natural selection was too weak to override the strength of harvest selection. However, natural selection favoring fast somatic growth strengthened across the time series in parallel with the increase in pike abundance and, presumably, cannibalism. Harvest selection was overridden by natural selection when the fishing effort dwindled, triggering a rapid increase in pike somatic growth. The two selective forces appear to have acted in concert during only one short period of prey collapse that favored slow-growing pike. Moreover, increased somatic growth occurred concurrently with a reduction in reproductive investment in young and small female pike, indicating a tradeoff between growth and reproduction. The age-specific amplitude of this change paralleled the age-specific strength of harvest pressure, suggesting that reduced investment was also a response to increased life expectancy. This is the first study to demonstrate that a consideration of both natural selection and artificial selection is needed to fully explain time-varying trait dynamics in harvested populations.

adaptive landscapes | conservation | contemporary evolution | fisheries | top predators

Selective harvest of the largest individuals may add a strong and temporally consistent directional component to the natural selective forces shaping adaptive landscapes (1). Theory predicts that such consistent selection should induce life history evolution (2–4). Accordingly, recent studies in nature indicate a correlation between increased harvest pressure and phenotypic changes in plants (5) and vertebrates (6). Harvest-induced phenotypic changes have been studied extensively in fisheries, where harvest is often associated with decreased somatic growth and/or decreased age and size at maturity (7–9). Under laboratory conditions, artificial selection against large size has been shown to induce rapid evolution toward slower growth (10) and to promote genetically based reductions in fecundity, larval viability, and foraging efficiency (11). These harvest-induced changes are generally considered maladaptive (11) because harvest and natural selection can act in different directions (1). However, to date, no study has examined the relative contributions of harvest and natural selection in driving trait changes in wild, harvested populations. We performed this task in pike (*Esox lucius*) from Windermere, U.K. This system is particularly well suited for this endeavor because we have previously

demonstrated that natural and fishery selection act in opposite directions on Windermere pike body size (1).

Windermere is a glacial valley lake divided by shallows into two basins of different productivity and constituting different habitats for pike (12, 13) (Fig. 1A). Commercial net fisheries for several species including pike have operated on Windermere since the 12th century but were terminated in 1921 because of heavy fishing problems (13). Le Cren (13) suggested that, by 1939, the fish population of Windermere consisted mainly of a dense population of perch (*Perca fluviatilis*) and a moderate population of pike feeding mostly on perch and, to a lesser degree, Artic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). Gillnet fishing for pike was initiated in 1944 with two objectives: (i) to 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 gillnets) 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 (in centimeters, measured as fork length), weighed (in kilograms), and 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 “checks”) 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 by 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

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Abbreviation: VBGC, von Bertalanffy growth curve.

[¶]To whom correspondence should be addressed. E-mail: n.c.stenseth@bio.uio.no.

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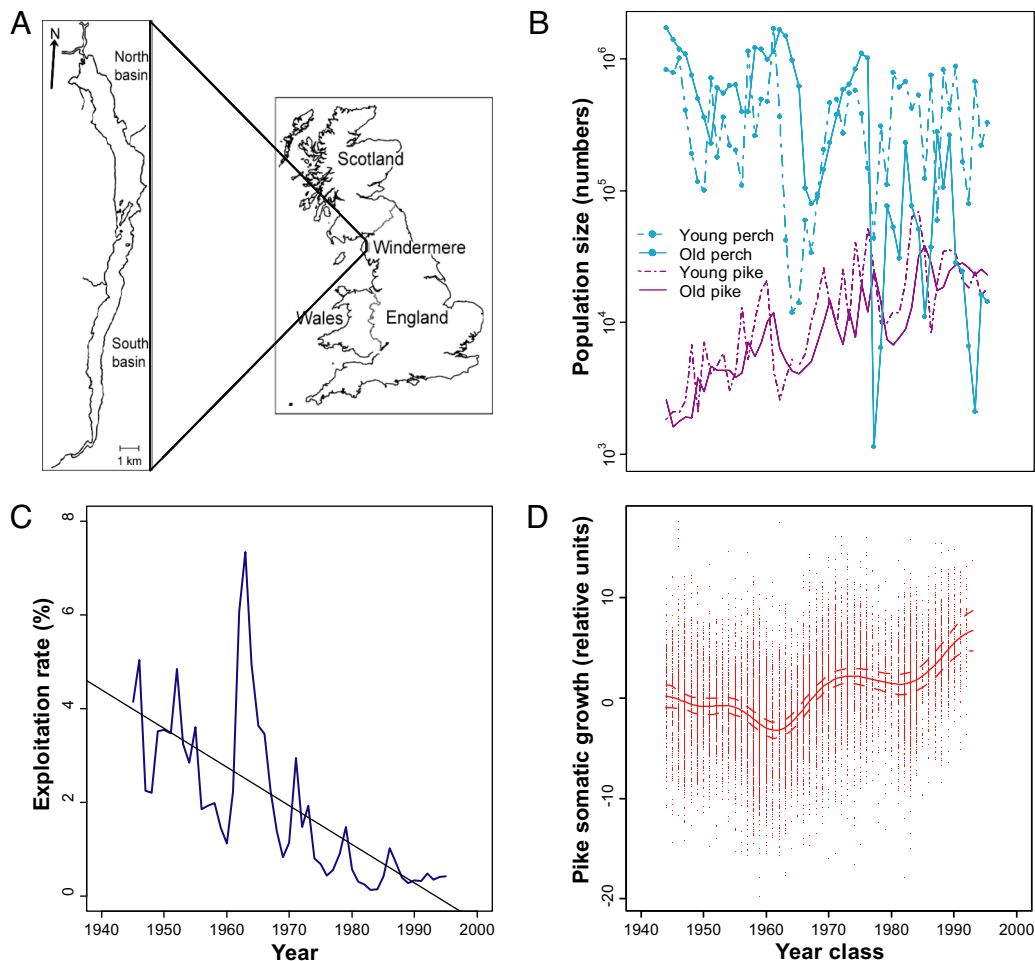


Fig. 1. Windermere background information and growth time series for pike (*E. lucius*). (A) Map showing the location of the study lake (surface area, 14.8 km²) in the Lake District of northwest England, U.K., and the division of the lake into two basins. The southern basin is morphologically different from and more productive than the northern basin. (B) Population size of pike (purple lines) and perch (thick blue lines with points) showing increased numbers of the predator and decreased numbers of the main prey (log₁₀ scale). Dashed lines represent “young” individuals (termed “young”), and solid lines represent age 3 and older individuals (termed “old”). (C) Exploitation rate for pike with trend line, representing the proportion of pike caught in the fishery during the winter compared with 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 variation 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 focal term from the model while leaving all other estimates fixed).

biological data, surface water temperatures were recorded on a nearly daily basis and were here averaged for each year. Finally, the abundance of pike and perch has been estimated annually for the 1944–1995 period, separately for each basin as well as separately for young (age = 2) and old (age > 2) individuals (17).

Natural and harvest selection have been previously quantified for the Windermere pike population through an estimation of the strength, direction, and form (directional, nonlinear) of the two selective forces (1). This earlier work demonstrated that harvest and natural selection often acted in opposite directions on pike body length (1). In particular, directional natural selection tended to favor large pike whereas the fishery targeted large individuals. Moreover, nonlinear natural selection tended to be stabilizing in Windermere, favoring pike of intermediate lengths, whereas fishery selection tended to be disruptive, favoring small and large pike (1). Large pike presumably have an advantage over small pike in terms of natural selection in that they are not susceptible to cannibalism, which can be severe in pike (18). Moreover, large pike likely have an advantage in terms of intrasexual combat for females during the breeding season (18).

The context for selection in Windermere changed across the five decades of study. From 1944 to 1995, pike numbers increased while perch numbers declined over the same period (Fig. 1B), likely resulting in increased agonistic interactions and cannibalism within the pike population. Consistent with this view, selection analyses indicate that stabilizing selection acting on Windermere pike body length overall strengthened through time (1) (i.e., that natural selection favoring fast somatic growth to reach the optimum length has increased). However, natural selection often fluctuates in

connection with severe environmental variations (19). In Windermere, collapse of the perch population due to a disease outbreak in 1976 (20) was likely the most severe environmental disturbance experienced by pike across the entire time series (Fig. 1B). Severe food stresses have been shown to select against fast growth (21). Therefore, ignoring fishery selection, we hypothesized that natural selection would drive an increase in pike somatic growth across the study period, except when the perch population collapsed in 1976. However, we also expected the fishery to simultaneously operate in the opposite direction and consistently drive decreased growth, but with a lesser effect when fishing intensity was reduced. Finally, if natural selection drove evolutionary change toward faster somatic growth, we would also expect a concurrent reduction in reproductive investment due to the tradeoff between growth and reproduction (2, 3).

To test these hypotheses in a robust framework, we used mixed-effects models (ref. 22; see also *Materials and Methods* for an extensive description of our models). In these models we have taken into account the many possible environmental variables (i.e., basin productivity, water temperature, pike numbers, and prey density) known to plastically affect somatic growth (e.g., increased abundance may reduce growth through a density-dependent food limitation). Additionally, because reproductive decisions are also functions of surplus energy gained before spawning (23), we have taken into account the effect of somatic body condition (hereafter “fatness”) in estimating changes in individual reproductive investment (see *Materials and Methods*). By considering the potential effects of harvest selection and natural selection, we demonstrate that both selective forces played a role in driving trait changes in Windermere pike across five decades.

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 (°C)	3.80 e-1	2.95 e+3 (1; 51,166)	<0.0001		
		Young pike (<i>n</i>)	1.63 e-4	7.86 e+3 (1; 51,166)	<0.0001		
		Old pike (<i>n</i>)	1.08 e-4	3.14 e+2 (1; 51,166)	<0.0001		
		Young perch (<i>n</i>)	-4.00 e-6	2.60 e+3 (1; 51,166)	<0.0001		
		Old perch (<i>n</i>)	-7.46 e-6	6.55 e+3 (1; 51,166)	<0.0001		
		Basin (two levels)	2.87 e-1	1.27 e+2 (1; 51,166)	<0.0001		
		Sex (females relative to males)	1.19 e+1	3.70 e+4 (1; 51,167)	<0.0001		
		Year (<i>n</i>)	1.58 e-1	1.65 e+5 (1; 51,167)	<0.0001		
		Temperature × young pike	-1.33 e-5	1.61 e+3 (1; 51,166)	<0.0001		
		Temperature × old pike	-1.60 e-6	7.80 e+3 (1; 51,166)	<0.0001		
		Temperature × young perch	4.05 e-7	1.46 e+3 (1; 51,166)	<0.0001		
		Temperature × old perch	7.14 e-7	2.12 e+3 (1; 51,166)	<0.0001		
		Sex × year	2.01 e-1	2.79 e+3 (1; 51,166)	<0.0001		
		ln gonad weight	Year (factor variable, 39 levels)	Month	-2.20 e-2	9.38 e+1 (1; 3,023)	<0.0001
<i>Kns</i> (somatic body condition)	6.20 e-3			4.94 e+1 (1; 3,023)	<0.0001		
ln length (cm)	4.01			7.21 e+3 (1; 3,027)	<0.0001		
Age (<i>n</i>)	-1.55 e-2			6.15 (1; 3,027)	0.0132		
Year (<i>n</i>)	-6.79 e-3			1.59 e+1 (1; 37)	0.0003		
ln length × age	1.59 e+1			2.49 e+1 (1; 3,023)	<0.0001		
ln length × year	8.15 e-2			7.00 e+1 (1; 3,023)	<0.0001		
Year × age	3.46 e-2			1.64 (1; 3,023)	0.2004		
ln length × year × age	-8.10 e-3			9.30 (1; 3,023)	0.0023		
Egg weight	Year (factor variable, 39 levels)			Month	-8.38 e-5	3.74 e+2 (1; 3,023)	<0.0001
				<i>Kns</i> (somatic body condition)	3.20 e-6	2.20 (1; 3,023)	0.1382
		ln length (cm)	1.43 e-3	2.98 e+1 (1; 3,027)	<0.0001		
		Age (<i>n</i>)	-9.33 e-6	2.88 e-1 (1; 3,027)	0.5915		
		Year (<i>n</i>)	-4.97 e-6	1.29 (1; 37)	0.2627		
		ln length × age	4.05 e-2	1.95 e-1 (1; 3,023)	0.6592		
		ln length × year	1.57 e-4	2.42 (1; 3,023)	0.1196		
		Year × age	8.33 e-5	9.62 (1; 3,023)	0.0019		
		ln length × year × age	-2.04 e-5	6.96 (1; 3,023)	0.0084		
		ln egg number	Year (factor variable, 39 levels)	<i>Kns</i> (somatic body condition)	4.96 e-3	4.75 e+1 (1; 3,024)	<0.0001
				ln length (cm)	3.56	3.62 e+3 (1; 3,028)	<0.0001
Age (<i>n</i>)	-1.34 e-2			8.80 (1; 3,028)	0.0030		
Year (<i>n</i>)	-3.32 e-3			8.3 (1; 37)	0.0065		
ln length × age	4.14			4.58 e+1 (1; 3,024)	<0.0001		
ln length × year	2.07 e-2			9.1 (1; 3,024)	0.0026		
Year × age	1.04 e-2			3.8 (1; 3,024)	0.0513		
ln length × year × age	-2.17 e-3			1.1 (1; 3,024)	0.2965		

*Parameter estimates for main effects are from models without interaction terms.

[†]Sequentially tested.

Results

We first tested for an overall change in pike somatic growth across the entire time series by modeling the linear effect of time on individual lifetime growth (asymptotic length; see *Materials and Methods*). We found that pike somatic growth increased significantly over the 1944–1995 period (Table 1). To evaluate shorter time-scale changes in relation to periods of varying strengths of natural and fishery selection, we modeled nonlinear changes in individual pike lifetime growth (Fig. 1D; see *Materials and Methods*). The nonlinear trend, shown in Fig. 1D, may be separated into four phases, which we describe below.

During the first phase, from 1944 to the early 1960s, somatic growth slightly decreased, suggesting that the selection imposed by fishing overwhelmed the strength of natural selection. There was a remarkably close match between the peak of fishing pressure in 1963 (Fig. 1C) and the slowest growth observed across the entire time series in year classes born from 1960 to 1963 (Fig. 1D) (i.e., year classes for which both the parents and the offspring experienced strong fishing pressure). During the second phase, 1963 to the

mid-1970s, pike somatic growth increased rapidly, suggesting that natural selection overwhelmed fishery selection during this time period (Fig. 1D). Pike somatic growth stabilized in fish born in the early 1970s, suggesting that phenotypic adjustment to the new adaptive peak took ≈ 10 years, a delay corresponding to two to five pike generations (i.e., Windermere pike first reproduce at age 2, but the mean generation time, calculated as the mean age of mature females weighed by their gonad weight, was estimated to be 5.2 years). During the third phase, from the mid-1970s through the mid-1980s, pike somatic growth decreased slightly, most likely because of an inversion in the direction of natural selection that then acted in concert with fishery selection. Indeed, in 1976 a disease outbreak induced a collapse of the perch population (20) whereas pike numbers were relatively high (Fig. 1B). Food stress might have thus induced starvation that ultimately selected against fast growth (21). The perch collapse was followed by a sharp decrease in pike numbers (Fig. 1B), supporting the view that prey shortage induced selection in the pike population through severe starvation. During the fourth phase, from the mid-1980s to the

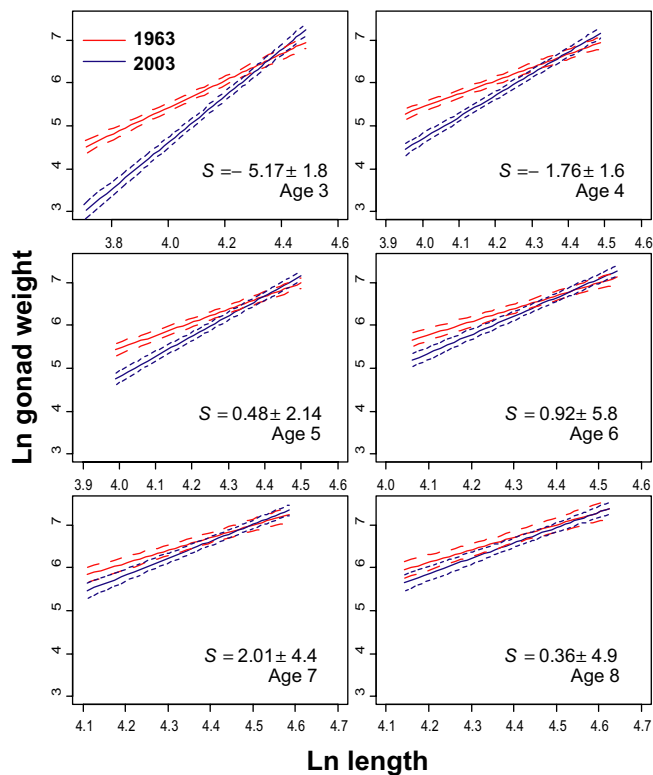


Fig. 2. Changes in the gonad weight/body length reaction norm of age 3 to age 8 female pike in Windermere. Lines represent predicted values for 1963 (bold, red) and 2003 (blue) with 95% confidence intervals (dotted lines) and were estimated from data for the 1963–1995 year classes. S is the age-specific mean selection differential (in centimeters \pm 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 \times 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 \times year \times age interaction in Table 1).

mid-1990s, pike somatic growth increased very rapidly, a period corresponding to the highest pike numbers observed across the time series, the lowest fishing pressure, and relatively low and fluctuating perch densities (Fig. 1 *B* and *C*).

Overall, this nonlinear trend confirms that fishery and natural selection were operating simultaneously and in opposite directions (1) and also supports the prediction that pike somatic growth variation responded to the dominant selective force. Fishery selection was overwhelmed by natural selection during the early 1960s (leading to the change from phase 1 to phase 2). Additionally, females grew faster than males overall and increased their growth rates at a faster rate than males over the study period (Table 1). This later result indicates that, as faster growers, females experienced stronger fishery selection than males and thus benefited more from the relaxation in the fishing pressure later in the time series. Finally, pike grew significantly faster in the more productive south basin compared with the less productive north basin (Table 1).

Concurrent with the increase in somatic growth after the early 1960s, we found that young, but not old, female pike reduced their reproductive investment (Fig. 2 and Table 1), providing support for our third hypothesis of a tradeoff between growth and reproduction in Windermere pike. Indeed, the age-specific intercept of the reproductive investment/length reaction norm decreased significantly for gonad weight and egg number, but not egg weight (Fig. 2 and Year effect in Table 1). Egg weight is positively correlated to

offspring size, and competition is predicted to favor large egg size (3). Hence, maintenance of egg weight despite decreased investment suggests increased competition in young pike in connection with increased pike density. At the same time, the age-specific slope of the investment/length reaction norm increased, indicating that female pike were investing in reproduction at a larger size (Fig. 2). This positive length \times year interaction was statistically significant for gonad weight and egg number but not egg weight (Table 1). In contrast, at any given length, the age at which investment occurred (age \times year interaction) increased significantly for egg weight only (Table 1). Finally, the magnitude of the aforementioned changes in investment decreased significantly with the age for both gonad weight and egg weight (Fig. 2 and length \times year \times age interaction in Table 1). To determine whether this length \times year \times age effect was related to age-specific differences in the relaxation of fishery selection after the early 1960s, we calculated age-specific mean fishery selection differentials for females at each age (see *Materials and Methods*). We found that fishery selection decreased with increasing age and was substantial on age 3 females only (Fig. 2), supporting the view that reduced reproductive investment was not only a response to strengthening natural selection but also related to increased life expectancy. Finally, somatic body condition had a positive effect on investment (significant on gonad weight and egg number) (Table 1), confirming that surplus energy gained before reproduction plastically affects energy allocation to reproduction (23).

Discussion

Wild populations are continually subject to natural selection, which temporally fluctuates in direction and/or magnitude (19). Natural selection acting on Windermere pike is presumably a function of both conspecific and prey (perch) densities. Before 1944, pike abundance was relatively low whereas perch were abundant (13), presumably creating conditions for weak competition for food and low cannibalism (i.e., weak natural selection for fast growth). However, throughout most of the time series under consideration, pike abundance was increasing while perch abundance was decreasing. These conditions set the stage for selection favoring fast growth presumably through cannibalism, because encounter rates between pike were increasing while prey abundance remained high enough to support fast growth in pike. However, the perch collapse in the mid-1970s seemed to reverse this trend during a short period by selecting for slow growth. This result provides support for previous work which suggested that nutrient stress is a strong agent of selection against fast somatic growth in both plants and animals (21). Together, these results suggest that the fitness of fast-growing pike as a function of the pike/perch ratio is dome-shaped in Windermere (i.e., for a pike, relatively large size confers fitness advantages as long as prey abundance is not too low). Cannibalism is generally considered as a “lifeboat” mechanism allowing populations to survive under decreased food conditions (24). Our results led us to modify this point of view by also suggesting that cannibalism can result in growth costs, which may be detrimental under very severe food stress.

The fishery for pike in Windermere consistently selected against fast growth, but the strength of this artificial selective force decreased across the time series. From the early 1940s to the early 1960s (phase 1), fishery selection was strong enough to override natural selection. The result was that combined selection favored decreased somatic growth during this time period. During phase 2 (\approx 10 years), relaxed fishing pressure allowed natural selection to prevail and resulted in combined selection favoring increased somatic growth. Phenotypic adjustment to the new adaptive optimum was remarkably fast (two to five generations). This result suggests that two slightly different evolutionary processes were at work. Average heritability for growth in fish ($h^2 = 0.3$) is high enough to cause substantial evolution in a few generations (25). However, because of the very detailed data used here we probably

also observed direct effects of the fishery (i.e., direct removal of fast-growing genotypes). Indeed, the slowest growth occurred in year classes that immediately preceded the peak of fishing pressure (i.e., in year classes that were born from parents that were strongly fished and that were themselves strongly fished). Consequently, relaxed fishing pressure immediately increased the proportion of fast-growing genotypes in the population. Interestingly, Carlson *et al.* (1) did not observe any significant change in the strength of directional selection acting on Windermere pike (i.e., selection pushing the population toward the newly emerging adaptive peak). They suggested that this was possibly due to pike quickly attaining equilibrium after fishing effort dwindled (1). Our results provide support for their assertion.

We show that a rapid shift toward fast growth after decreased fishing pressure was accompanied by a reduction in reproductive investment in young and small females. This result strongly supports the prediction of a genetic tradeoff between growth and reproduction in Windermere pike (2, 3). Importantly, we have accounted for the plastic effect of short-term variation in growth conditions in our reaction norm approach. Indeed, in teleosts plasticity in reproductive decisions is affected by the rate of surplus energy gained during critical periods (23). In Windermere pike, energy used for reproduction in March and April is gained during the previous summer (15). We have here estimated surplus energy gained during the previous summer as the somatic body condition (fatness) at capture, and we show that condition had a positive effect on investment. After accounting for this plastic effect, we found that investment at each reproduction decreased while the length at which investment occurred increased. We further show that the age-specific amplitude of this later change paralleled the age-specific strength of fishing selection, suggesting that investment change was partially a response to relaxation in the fishing pressure. Hence, our results provide further support for previous research, which suggested that fisheries may induce genetic change in the energy allocation rules to growth and reproduction in fish populations (2, 4). Instead of investing in gonads early in life and at a small size because of fishery-induced mortality, Windermere female pike now grow first to increase fitness through the achievement of a larger body size.

Our data suggest that pre-1963 exploitation rates of 1.1–7.3% (mean = 3.3%) were enough to impede the effects of natural selection in Windermere pike and even cause detectable evolution in the opposite direction. It is thus highly probable that commercial harvest, which may deplete 45–99% of the reproductive biomass (26), may cause rapid evolution in commercial fish stocks. Temporal consistency of harvest practices (e.g., systematic removal of the largest individuals) likely magnifies the evolutionary impacts of exploitation. Introducing variety in harvest practices could limit the amplitude of harvest-induced trait changes. However, our results point out that knowing the intensity and direction of artificial selection is not always enough to predict the response of populations to harvest. Instead, trait changes result from the combined forces of both the harvest and natural selection, and evolution of harvested populations is thus a process more complex than generally portrayed. Conservation plans that ignore this complexity could lead to improper management decisions.

Materials and Methods

Growth Modeling. We tested for linear change in growth during the 1944–1995 period using a nonlinear mixed-effects model (random grouping factor $n = 13,942$ individuals, $n = 65,123$ observations). This model was based on the von Bertalanffy growth curve (hereafter VBGC, fitted to length-at-age data for each individual) and allowed us to quantify the temporal trend in individual asymptotic length. Asymptotic length is an index of lifetime somatic growth rate. The index thus synthesizes an individual's decisions for energy allocation and is particularly powerful to study life-history variation and evolution. The trend in asymptotic length was estimated while simultaneously controlling for the effect of basin productivity and

the effects of yearly variation in water temperature, prey numbers, and pike numbers. Individual pike growth was modeled with a three-parameter formulation of the VBGC (27): $L(A) = \alpha + (\beta - \alpha)\gamma^A$, where L = length (in centimeters), A = age, β = intercept, γ = rate of increase, and α = asymptotic length. This formulation of the VBGC yielded the lowest Akaike's information criterion and less structure in the residuals compared with six other formulations of the VBGC and eight other nonlinear models [the Gompertz, three- and four-parameter logistic, Pauly's, Morgan, Mercer and Flodin, Weibul, modified Freundlich, Chapman–Richards, and Michaelis–Menten models (27)]. The selected VBGC equation was incorporated into a restricted maximum likelihood nonlinear mixed-effects model (22) [NLME library of R (28)]:

$$L_{ij} = \alpha_{ij} + (B - \alpha_{ij})\gamma^{A_i} + \varepsilon_{ij}, \quad [1]$$

where L_{ij} is length of individual i in year j , ε_{ij} is a normally distributed within-individual error term, and the parameter α_{ij} is associated with fixed covariate effects and a random individual effect:

$$\begin{aligned} \alpha_{ij} = & \beta_0 + \beta_1 T_j + \beta_2 Y_{pij} + \beta_3 O_{pij} + \beta_4 Y_{pej} + \beta_5 O_{pej} + \beta_6 Bas_i \\ & + \beta_7 S_i + \beta_8 Y_i + \beta_9 T_j \cdot Y_{pij} + \beta_{10} T_j \cdot O_{pij} + \beta_{11} T_j \cdot Y_{pej} \\ & + \beta_{12} T_j \cdot O_{pej} + \beta_{13} Y_j \cdot S_i + b_i, \end{aligned} \quad [2]$$

where β_s = model coefficients for the fixed-effects part where Y is year, S is sex, Bas is basin, T is temperature, Y_{pi} is young pike (age = 2), O_{pi} is old pike (age > 2), Y_{pe} is young perch (age = 2), O_{pe} is old perch (age > 2), and b_i is a normally distributed random individual effect. Interaction between temperature and each biological covariate accounted for the thermal dependence of food conversion efficiency and predator–prey overlap and generated significant improvement of model Akaike's information criterion compared with a simple additive formulation. Estimates of the main effects of Y and S (Table 1) were obtained from a model in which the year \times sex interaction was omitted from Eq. 2. Both models incorporated within-individual temporal autocorrelation (autoregressive function of time of order 1) and handled heteroscedasticity by modeling the variance of ε_{ij} as the product of a sex-specific power function of A and a linear function of Y . Fig. 1D was obtained from a generalized additive mixed-effects model [GAMM, mgcv library of R (29)] in which individual asymptotic length (α_i) was the response [computed from a model similar to Eqs. 1 and 2, except that the fixed-effects part did not contain any covariate ($\alpha_i = \beta_0 + b_i$ in Eq. 2)], grouped by S , nested in Bas_i , nested in *year class* (random grouping factor $n = 197$ groups, $n = 13,942$ individuals). In the GAMM, predictors were as in Eq. 2 with no year \times sex interaction, covariates were averaged across each individual's life, and the linear Y effect was replaced by a nonlinear *year class* effect (natural quadratic spline), thus removing any *a priori* expectation concerning the shape of the trend.

Reproductive Investment Modeling. We tested for temporal changes in the slope and intercept of the reproductive investment/body length reaction norm of females born from 1963 to 1995 using linear mixed-effects models including the full interaction among length, age, and time as continuous variables (random grouping factor $n = 41$ years, $n = 3,070$ observations). Rep_{ij} represents gonad weight, egg number (both ln-transformed), or egg weight of individual i in year j and were modeled with restricted maximum likelihood linear mixed-effects models:

$$\begin{aligned} Rep_{ij} = & \beta_0 + \beta_1 A_{ij} + (\beta_2 + b_1) \ln L_{ij} + \beta_3 Y_j + \beta_4 M_i + \beta_5 K n s_i \\ & + \beta_6 \ln L_{ij} \cdot Y_j + \beta_7 A_{ij} \cdot \ln L_{ij} + \beta_8 Y_j \cdot A_{ij} + \beta_9 A_{ij} \cdot \ln L_{ij} \cdot Y_j \\ & + b_2_j + \varepsilon_{ij}, \end{aligned} \quad [3]$$

where β are model coefficients for the fixed-effects part, b_{1j} and b_{2j} are normally distributed random year effects (with a symmetric covariance matrix), and ε_{ij} is a normally distributed within-year error term. Fixed-effect covariates were as follows: A is age, $\ln L$ is the natural log of length (in centimeters), Y is year (continuous variable), and M is month of capture (from October to February). Kns is the relative somatic condition factor (30): $Kns = 100 \times SM/SM_{std}$, where SM is the somatic mass (total mass – gonad mass) and SM_{std} is the predicted somatic mass of a fish of the same length L , as calculated from the $\ln(SM) - \ln(L)$ regression equation (least-squares mean fit, $n = 3,694$; $R^2 = 0.96$). Somatic body condition was found to have a stronger effect on reproductive investment than previous growth history (α and last growth increment) during model selection procedure based on Akaike's information criterion. The M effect on egg number was not significant and was thus omitted from egg number modeling. Estimates of the main effects of $\ln L$, A , and Y (Table 1) were obtained from a model in which the interactions were omitted from Eq. 3. The models handled heteroscedasticity by modeling the variance of ε_{ij} as the

product of exponential functions of A and $\ln L$. Predicted values in Fig. 2 were computed from the interaction model. Finally, selection differentials provided in the reproductive investment analysis and in Fig. 2 were estimated for each year and each age as the mean back-calculated length of females that escaped the fishery in that year (but were caught eventually) minus the mean length of females of the same age caught into the fishery in that year (9) for the entire study period (1945–1995).

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