



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 Chr. Stige, Ian J. Winfield, Janice M. Fletcher, Ben J. James, Thron O. Haugen, Asbjørn L. Vøllestad, Nils Chr. Stenseth

► To cite this version:

Eric Edeline, Stephanie M. Carlson, Leif Chr. Stige, Ian J. Winfield, Janice M. Fletcher, et al.. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences of the United States of America*, 2007, 104 (40), pp.15799-15804. 10.1073/pnas.0705908104 . bioemco-00353091

HAL Id: bioemco-00353091

<https://hal-bioemco.ccsd.cnrs.fr/bioemco-00353091>

Submitted on 31 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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, Library Avenue, Bailrigg, Lancaster, Lancashire LA1 4AP, United Kingdom; and §Norwegian Institute for Water Research, Gaustadalléen 21, 0349 Oslo, Norway

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved August 23, 2007 (received for review June 23, 2007)

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, Arctic 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

Author contributions: E.E., T.O.H., L.A.V., and N.C.S. designed research; E.E., S.M.C., L.C.S., I.J.W., J.M.F., J.B.J., and T.O.H. performed research; E.E., S.M.C., and L.C.S. analyzed data; and E.E. and S.M.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Abbreviation: VBGC, von Bertalanffy growth curve.

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

© 2007 by The National Academy of Sciences of the USA

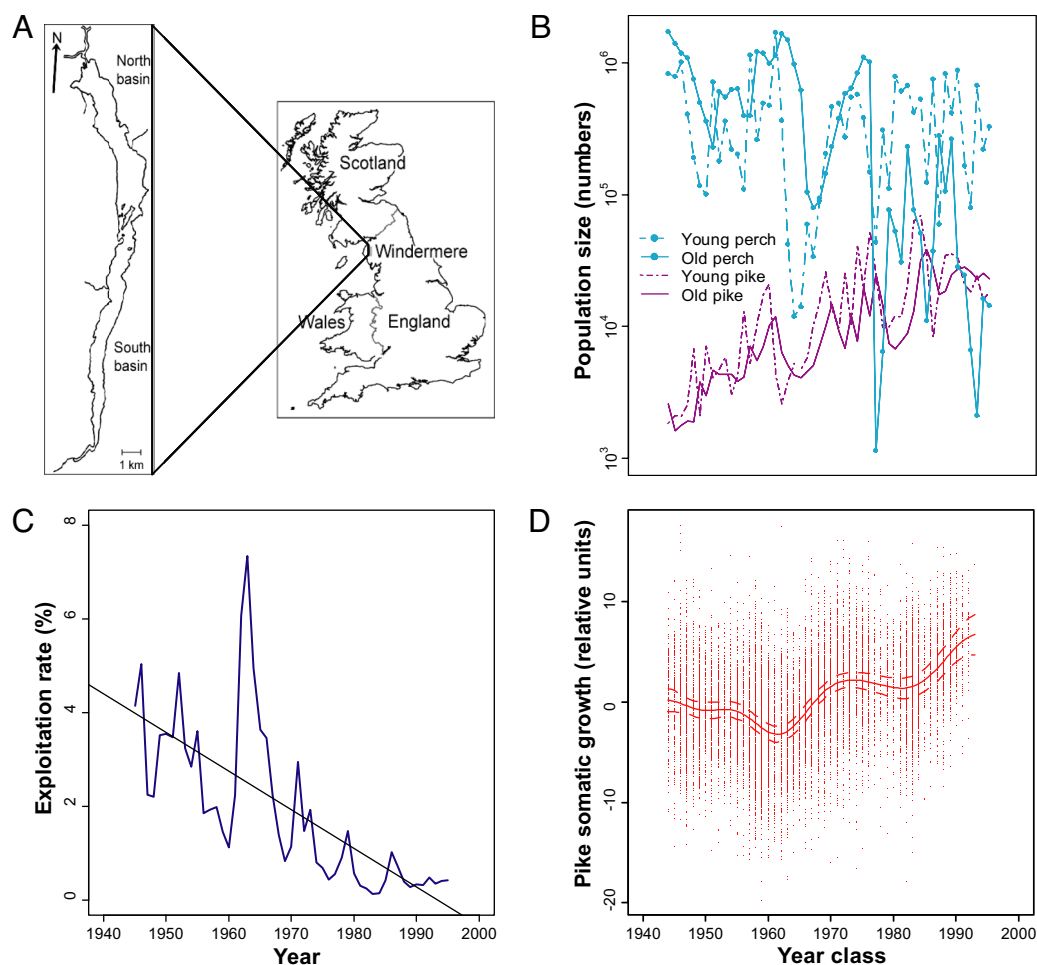


Fig. 1. Windermere background information and growth time series for pike (*E. lucius*). (A) Map showing the location of the study lake (surface area, 14.8 km²) in the Lake District of northwest England, U.K., and the division of the lake into two basins. The southern basin is morphologically different 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 age 2 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.

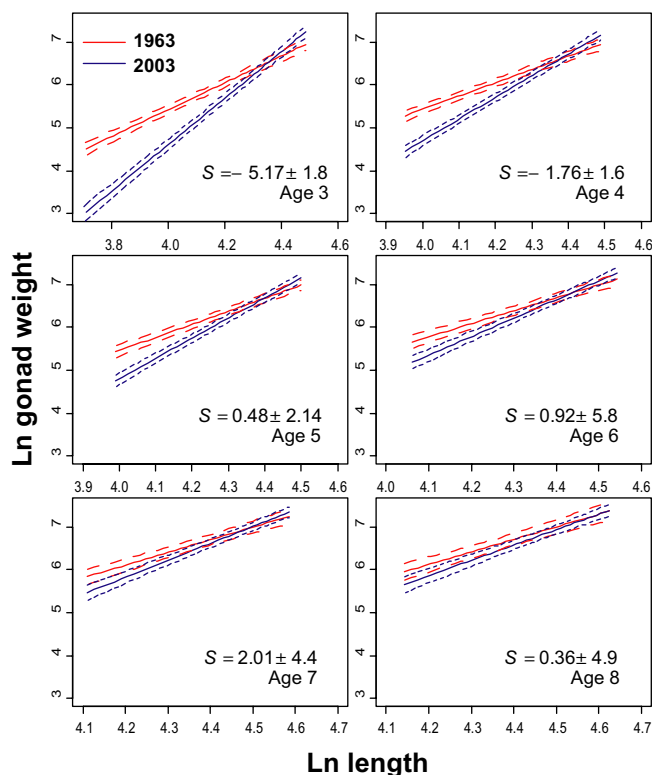


Fig. 2. Changes in the gonad weight/body length reaction norm of age 3 to age 8 female pike in Windermere. Lines represent predicted values for 1963 (bold, red) and 2003 (blue) with 95% confidence intervals (dotted lines) and were estimated from data for the 1963–1995 year classes. S is the age-specific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

