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LETTER

Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*)

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Abstract

The ability of natural selection to drive local adaptation has been appreciated ever since Darwin. Whether human impacts can impede the adaptive process has received less attention. We tested this hypothesis by quantifying natural selection and harvest selection acting on a freshwater fish (pike) over four decades. Across the time series, directional natural selection tended to favour large individuals whereas the fishery targeted large individuals. Moreover, non-linear natural selection tended to favour intermediate sized fish whereas the fishery targeted intermediate sized fish because the smallest and largest individuals were often not captured. Thus, our results unequivocally demonstrate that natural selection and fishery selection often acted in opposite directions within this natural system. Moreover, the two selective factors combined to produce reduced fitness overall and stronger stabilizing selection relative to natural selection acting alone. The long-term ramifications of such human-induced modifications to adaptive landscapes are currently unknown and certainly warrant further investigation.

Keywords

Fishery selection, fitness functions, harvest, natural selection, opposing selection, size selection, survival.

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INTRODUCTION

The power of natural selection to drive evolution and local adaptation has long fascinated evolutionary biologists. Less work has examined whether human impacts can impede natural adaptive processes, such as by introducing opposing selection pressures. One impact that can have profound effects on the demographic and evolutionary dynamics of natural populations is trait-selective harvesting done by humans. For instance, the collapse of northern cod (*Gadus morhua* Linnaeus) was preceded by changes in age- and size-at-maturity that were congruent with predictions from life-history theory; fish continually matured at a younger and smaller size until fishing ceased (Olsen *et al.* 2004). Similarly, trophy hunting of bighorn rams (*Ovis canadensis* Shaw) has been shown to result in a decrease in body weight and horn size (Coltman *et al.* 2003) because males with the most rapidly grown horns were targeted. Although these studies demonstrate that trait-selective harvest can produce evolutionary changes, they do not provide information on the degree that human-induced selection operated in opposition to natural selection.

Opposing artificial selection has several potential implications for wild populations. First, opposing artificial selection might promote the maintenance of non-naturally optimal phenotypes and, thus, prevent the population from reaching its natural selection optimum. Second, if a population has yet to attain evolutionary equilibrium, this should maintain strong directional natural selection to push the mean trait value towards the natural selection optimum trait value. Finally, opposing artificial selection might warp the adaptive landscape. For instance, if the form of human-induced selection differs from the form of natural selection acting on a trait, the adaptive landscape will reflect the combined selective pressures. In short, we suggest that opposing human-induced selection may hinder natural adaptive processes. With these potential implications of opposing artificial selection in mind, we estimated natural selection and fishery selection acting on northern pike (*Esox lucius* Linnaeus) in Windermere (UK) over four decades.

No previous study has tested the prediction that natural and human-induced selection act in opposite directions. Our study can evaluate this prediction effectively for a number of reasons. First, our study is unique in that we estimated both natural selection and human-induced selection acting within a single system. Second, our *a priori* expectation is that natural selection will favour large fish whereas fishery selection will favour small fish. This expectation arises because large body size confers fitness benefits in pike [increased fecundity (Wright & Shoesmith 1988) and egg size in females (Frost & Kipling 1967); increased gape size (Magnhagen & Heibo 2001)] but previous work has suggested the Windermere pike fishery removes the largest individuals (individuals longer than 55 cm are susceptible to a scientific gill net fishery, Frost & Kipling 1967). We therefore predicted that natural selection and fishery selection would act in opposite directions in this system. Third, our study is exceptional in that our results are temporally replicated, providing an opportunity to assess their generality. The benefits of long-term studies of selection in nature are becoming increasingly recognized but, nevertheless, such studies are rare. Indeed, most studies of selection in nature are not temporally replicated (Kingsolver *et al.* 2001). This is unfortunate because long-term selection studies have revealed that selection pressures fluctuate temporally (Grant & Grant 1995, 2002; McAdam & Boutin 2003; Carlson & Quinn 2007) and it therefore seems dubious to make generalizations about the strength and form of selection based on unreplicated estimates of selection.

We employed traditional methods to estimate standardized directional and quadratic selection differentials (see Materials and methods) across four decades in Windermere pike. In particular, we generated year-specific estimates of natural selection and fishery selection acting on pike body size. This set the stage for testing the prediction that natural selection and fishery selection acted in opposite directions *within a given year*. We predicted that the two selective factors would often oppose one another because the many benefits of large body size in pike (see above) likely increase an individual pike's susceptibility to capture by the fishery. Finally, we estimated the fitness function due to natural selection alone, fishery selection alone, and the combined fitness function (natural selection × fishery selection, Arnold & Wade 1984). This allowed us to directly assess the impact of human-induced selection on pike fitness. We show that human-induced selection has often acted in the opposite direction as natural selection and has altered the fitness landscape in this system by reducing fitness overall and magnifying the strength of stabilizing selection throughout the time series.

MATERIALS AND METHODS

Pike were sampled in Windermere, UK (latitude 54.37 °N, longitude 2.94 °W) as part of a long-term scientific monitoring program. Details about this lake can be found in Kipling (1984). Individual pike were captured prior to and during the spring spawning period (March–April) with gillnets (38 and 64 mm) and perch (*Perca fluviatilis* Linnaeus) traps, all untagged fish were tagged with loops of monel metal which were punched with a six-digit unique identifier (Kipling & Le Cren 1984), all fish were measured for body length (tip of the snout to the fork in the caudal fin; 'spring length'), and released alive. The combination of capture methods (38 and 64 mm mesh size gill nets and perch traps) facilitated the capture of mature pike across a representative range of body sizes. As part of the monitoring program, a scientific fishery for pike in Windermere has taken place between October and February each year since 1944 (in recent decades this has occurred almost exclusively between October and December). With the exception of some unknown accidental mortality in catch-and-release angling (the number of anglers on the lake is small), this is the only source of fishing mortality for pike in Windermere. During this fishery, pike were captured in gillnets (mesh size = 64 mm) and were killed, regardless of whether they had been tagged previously or not. Our analyses were based on two data sets. The first was used to estimate the strength and form of *natural* selection acting on Windermere pike. This data set was based on the capture–mark–recapture (CMR) data. This data set has been described extensively in two recent papers (Haugen *et al.* 2007; Haugen *et al.* 2006; see also Morris 2006), and we present only those details pertinent to the present analysis. The second data set was used to estimate the strength and form of *fishery* selection acting on Windermere pike. This data set was based on back-calculated length-at-age data (see 'Fishery selection') determined for fish killed during the winter fishery. This combination of data sets allowed a direct test of the strength and form of both natural selection and harvest-induced selection in a natural system.

Natural selection

We used standard procedures (Lande & Arnold 1983; Brodie *et al.* 1995; Janzen & Stern 1998) to estimate the strength and form of size-related selection in Windermere pike in each of 34 summers (1953–1986, summer loosely defined as the period between May and September). For each year, we tested whether survival through the summer was related to body size in the spring (i.e. body size at the beginning of the summer). Thus, all individuals captured in a particular spring were included in the analysis for that year (i.e. we tracked their fates). Fish captured at the end of the summer in the fishery, or in any subsequent sample, were assigned an absolute fitness of unity. Fish that were never captured again were considered dead and assigned an absolute fitness of zero (Letcher *et al.* 2005). Some of these fish may have survived the focal period but the combination of numerous sampling occasions (see Appendix S1 in Supplementary Material), the long lifespan of Windermere pike (up to 17 years, Frost & Kipling 1967), and the fact that Windermere is a closed system for pike minimized this possibility. To maximize sample sizes for analyses, we did not partition the CMR data set by size or sex (note, however, that 65% of the observations in the CMR data set represent male pike). Relative fitness was then determined for each individual as its absolute fitness (0 or 1) divided by the mean absolute fitness of all individuals for that year. The opportunity for selection (I) in each year was calculated as the variance in relative fitness (Brodie *et al.* 1995).

We estimated univariate selection during each summer as regressions of fitness on standardized body length (standardized to a mean of zero and a standard deviation of unity; hereafter 'body length'). We used two sets of regressions to estimate the strength and form of selection acting on Windermere pike. Due to the dichotomous nature of the response variable, logistic regressions were performed in each case (Janzen & Stern 1998). First, we performed simple logistic regressions of fitness on body length. Coefficients from these regressions estimate directional (logistic) selection differentials, which represent the total strength of selection acting on body length. Second, we performed regression of fitness on body length plus its squared term. The quadratic coefficients from these regressions estimate quadratic (non-linear) selection differentials, which are typically interpreted as representing disruptive (when positive) or stabilizing (when negative) selection. Finally, we tested for a temporal trend in the selection coefficients using ordinary least squares regression.

Fishery selection

Data included in the fishery selection analyses were based on back-calculated lengths-at-age. At capture during the fishery, body length (fork length) was measured, sex was recorded, and the opercular bone was removed for subsequent ageing. Body lengths at the end of each previous growing season (i.e. 'lengths-at-age') were estimated from the opercular bone. If a fish was captured in the fishery and killed at age-6, for instance, the age-6 length was measured and the age-1 to age-5 lengths were estimated based on the opercular bone size at previous ages and a relationship between opercular bone size and body size established for the Windermere pike population (Frost & Kipling 1959). This ageing technique has been validated for Windermere pike by comparing the measured length of a subset of fish that were previously captured, measured, and released alive to the back-calculated length at that age based on the opercular bone (Frost & Kipling 1959; Kipling 1983).

Given the large number of data points in the back-calculated length database (total $n = 14,648$), we were able to run sex- and age-specific fishery selection analyses. We limited our analyses to the age-classes that were must vulnerable to capture by the fishery (Frost & Kipling 1967) and to age-classes with sample sizes large enough to ensure a robust analysis of selection. We thus focused our analyses on two age-classes for each sex (females: age-3 and age-4; males: age-4 and age-5). Each cohort and sex combination was sampled in multiple years (i.e. females from the 1953 cohort were captured at age-3 during the 1955 fishery, age-4 during the 1956 fishery, and so on), which facilitated a comparison of the strength of fishery selection as a cohort aged/grew. For a given cohort and sex, we determined whether the probability of being captured in the fishery at age-4, for instance, was related to age-4 body length. Following the approach of Sinclair *et al.* (2002), we performed this task by comparing the body length of the subset of individuals captured at age-4 (fitness = 0) to the back-calculated age-4 length of individuals that were not captured at age-4 (fitness = 1) but were instead captured at some later age. Selection analyses proceeded as before (i.e. regressions) to determine the strength and form of fishery selection.

Fitness functions

We visualized the form of natural selection and fishery selection acting on body length via univariate cubic splines (Schluter 1988). As Sinclair *et al.* (2002), we generated these splines within the program R (GAM function) in which the smoothing parameter is selected by generalized cross-validation. For a subset of the natural selection data, we compared the predicted values from program R with predicted values from Schluter's spline program (glms WIN 1.0 spline program) and found a high degree of correspondence (R^2 ranged from 0.95 to 0.99 for five randomly selected years). For the fishery selection analysis, we used data on all fish captured in the fishery in a given year (i.e. both sexes and all ages) to visualize the strength and form of fishery selection acting on Windermere pike. Finally, we visualized total selection by calculating the product of the natural selection and fishery selection fitness functions (Arnold & Wade 1984). In particular, this was accomplished by calculating the product of the predicted fitness from the natural selection GAM by the predicted fitness from the fishery selection GAM.

RESULTS

Natural selection

To estimate natural selection acting on pike body length, we analysed 4602 observations of summer survival in combination with spring body length across 34 years (note that the total number of individuals was less than the number of observations as some individuals were recaptured on multiple occasions). Of these, 2483 observations represented individuals known to have survived the focal summer (i.e. individuals that were recaptured in the winter fishery or sometime thereafter). The per cent of individuals surviving the focal summer period ranged from 26% to 75% among years and the opportunity for selection ranged from 0.34 to 2.86 (Table 1). Details on year-specific natural selection analyses can be found in Appendix S2, Table S2.

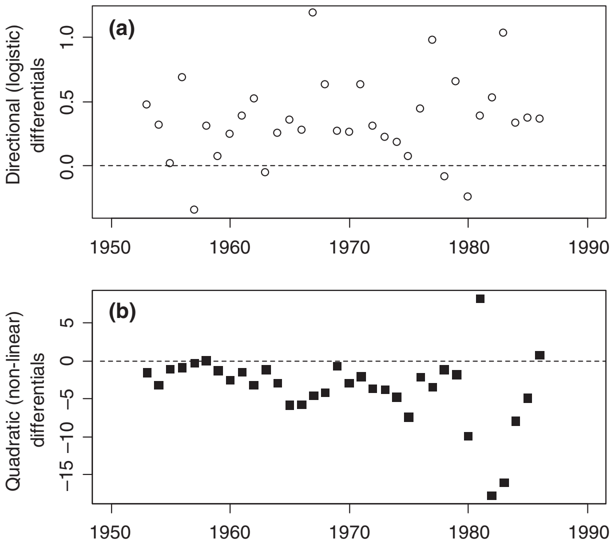

Figure 1 The direction and magnitude of directional (a) and non-linear (b) natural selection acting on Windermere pike. Positive directional coefficients suggest that large fish were favoured. Negative non-linear coefficients suggest that selection was often stabilizing (i.e. fish of intermediate lengths had the highest fitness). Together, these results suggest that large fish were favoured overall but that the largest fish did not have the highest fitness. For ease of interpretation, we have plotted only the selection coefficients and have included standard errors and *P*-values in Appendix S2 and Table S2. The dashed horizontal line at $y = 0$ indicates no selection on pike body length.

Several general patterns emerged with regards to natural selection acting on Windermere pike. First, selection was remarkably consistent in direction across the time series: directional selection favoured the largest fish (Fig. 1(a); Appendix S2, Table S2) and quadratic selection was stabilizing (Fig. 1(b); Appendix S2, Table S2). This latter result suggests that fish of intermediate lengths were favoured. Second, selection was often strong [directional selection was significant in 12 years (*P*-value < 0.05) and was marginally significant in another 4 years (*P*-value < 0.10); quadratic selection was significant in 13 years (*P*-value < 0.05) and was marginally significant in one additional year (*P*-value < 0.10)]. Nevertheless, there was some evidence for a lack of power to detect selection in our data set as analyses revealing strong (significant) selection tended to be

Table 1 Summary of the results from our analyses of natural selection and fishery selection acting on Windermere pike. We present summary information on the per cent of individuals surviving the focal period (i.e. recaptured after the focal period), the opportunity for selection (i.e. the variance in relative fitness), logistic and quadratic differentials. These summary results are presented as the average ± standard deviation, with the range among years indicated directly below in parentheses. For the fishery selection analysis, results are partitioned by sex and by age. Information on year-specific analyses can be found in Appendix S2, Tables S2–S6.

Sex	Age	Survived focal period (%)	Opportunity for selection (*I*)	Directional (logistic) differentials	Quadratic (non-linear) differentials
Natural selection					
NA	NA	52.44 ± 10.30	1.02 ± 0.57	0.36 ± 0.33	−3.58 ± 4.56
		(26.47 to 74.76)	(0.34 to 2.86)	(−0.35 to 1.19)	(−17.79 to 8.28)
Fishery selection					
Female	3	72.60 ± 16.78	0.47 ± 0.40	−1.57 ± 0.75	15.42 ± 15.61
		(40.96 to 98.58)	(0.01 to 1.45)	(−3.57 to −0.42)	(−15.05 to 67.02)
Female	4	41.00 ± 14.54	1.76 ± 0.97	−0.41 ± 0.44	7.59 ± 8.56
		(20.25 to 92.08)	(0.09 to 3.99)	(−1.52 to 0.25)	(−22.80 to 23.76)
Male	4	65.23 ± 16.22	0.65 ± 0.49	−1.49 ± 0.61	18.93 ± 24.40
		(33.00 to 94.06)	(0.06 to 2.04)	(−2.70 to −0.40)	(−9.97 to 141.48)
Male	5	47.31 ± 12.44	1.27 ± 0.59	−0.72 ± 0.54	15.13 ± 18.16
		(24.62 to 92.00)	(0.09 to 3.11)	(−2.22 to 0.47)	(−6.80 to 84.36)

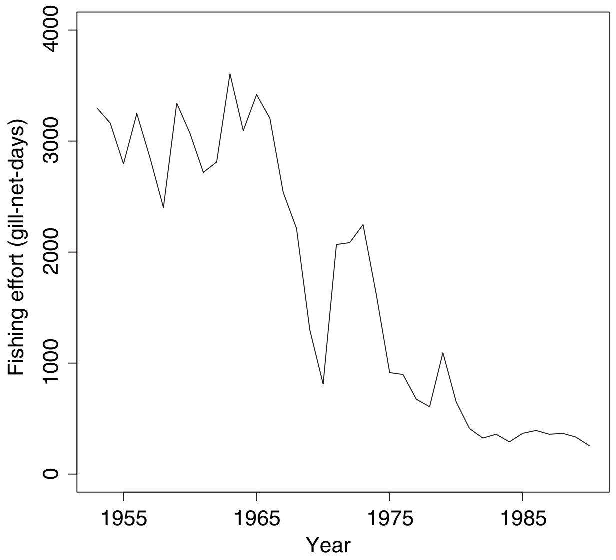

Figure 2 Fishing effort (i.e. number of gill-net-days in a given year) from 1953 to 1990.

associated with larger sample sizes than analyses yielding non-significant selection coefficients (Appendix S2, Table S2). Finally, we tested for a trend in the directional and quadratic selection differentials. To do this, we first performed an autoregressive time series analysis to test for evidence of autocorrelation in the two data sets. Given the lack of autocorrelation in the data (directional selection differentials: $P = 0.26$ for the first-order autoregression coefficient; quadratic selection differentials: $P = 0.57$ for the first-order autoregression coefficient), we next performed ordinary least squares regressions to test for a temporal trend. This approach revealed that the directional selection differentials showed no temporal trend (slope = 0.006, $R^2 = 0.03$, $P = 0.323$) whereas quadratic selection differentials became increasingly negative through time (slope = −0.157, $R^2 = 0.12$, $P = 0.048$). This latter result is likely a direct effect of the reduction in fishing towards the end of the time series (Fig. 2). That is, more individuals reach advanced ages/grow larger later in the time series suggesting a larger range of body lengths for selection to act on relative to earlier in the time series.

Fishery selection

For the 38 years included in the fishery selection analysis (1953–1990), survival through the fishery averaged 73% and 41% for age-3 and age-4 females, respectively, and 65% and 47% for age-4 and age-5 males, respectively (Table 1). Note that *all* of these fish were eventually captured and killed during the fishery. See Appendix S2, Tables S3–S6 for year-specific information regarding the per cent captured at a given age as well as the opportunity for selection.

Several noteworthy patterns emerged with regards to fishery selection on Windermere pike. First, the fishery was highly selective on the basis of size, particularly for the youngest (i.e. smallest) fish (Table 1). When pike first recruited to the fishery, the fishery removed the largest individuals (i.e. directional differentials were *always* negative, Fig. 3; Appendix S2, Tables S3 and S5). Moreover, directional selection was strong. For both females (age-3) and males (age-4), 36 of the 38 directional coefficients generated for each sex were significant ($\alpha = 0.05$; Appendix S2, Tables S3 and S5). Second, selection on length changed with age. In particular, the directional coefficients became weaker (i.e. less negative) as a cohort aged (Fig. 3, left panels). This is due to the fact that fish are larger at each subsequent age but the relationship between gill net selectivity and length is constant. Thus, for the youngest (smallest) fish, relatively large individuals were captured by the fishery but this pattern was dampened as the fish aged/grew. This pattern suggests that the largest individuals of a cohort were not the individuals most susceptible to capture in the fishery. Indeed, quadratic selection coefficients (Fig. 3, right panels) tended to be positive suggesting that fishery selection on pike body length was disruptive (i.e. the smallest and largest pike were less likely to be captured). Moreover, this result was consistent across ages and sexes (Fig. 3, right panels).

Fitness functions

Inspection of fitness surfaces (i.e. the form of selection) revealed that natural selection was often stabilizing, with fish *c.* 60 cm in length having the highest fitness, and that fishery selection was often disruptive, with fish near 65 cm in length often having reduced fitness relative to smaller and larger individuals (Fig. 4). Within a given year, natural selection and fishery selection often acted in opposite directions (e.g. 1954, 1962, 1966, 1968, 1970, 1972, 1973, 1978 of Fig. 4). By comparing the fitness surface due to total selection (natural selection × fishery selection) to that due to natural selection acting alone, it was possible to determine the direct impact of fishery-induced selection on the fitness surface. This revealed that fishery selection lowered the fitness surface (i.e. reduced fitness) overall, particularly for fish longer than 55 cm (Fig. 5). By subtracting the two fitness functions over the common range of body lengths, we found that the addition of fishery selection reduced absolute fitness by 0.15 on average across years (range across years: 0.05 [1985]–0.30 [1976]; note that absolute fitness ranges between zero and unity). Moreover, fishery-induced selection tended to magnify the strength of stabilizing selection overall (Fig. 5), because the fitness of relatively long individuals was reduced in the presence of the fishery.

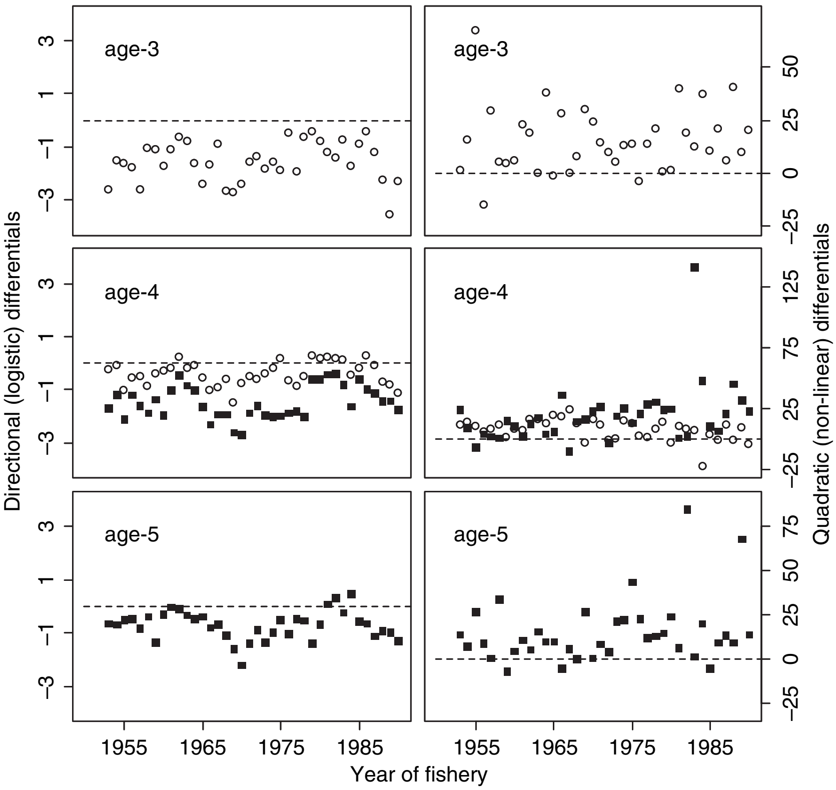

Figure 3 Fishery selection coefficients plotted against year of the fishery as a function of both age and sex (females: open circles; males: black squares). Directional coefficients are plotted in the left panels and non-linear coefficients are plotted in the right panels. Positive (negative) directional coefficients suggest that large (small) fish were favoured. Positive (negative) non-linear coefficients suggest disruptive (stabilizing) selection on pike body length. For ease of interpretation, we have plotted only the selection coefficients and have included standard errors and *P*-values in Appendix S2, Tables S3–S6. The dashed horizontal line at $y = 0$ indicates no selection on pike body length.

DISCUSSION

Our analyses clearly demonstrate that natural selection and human-induced selection often acted in opposite directions in Windermere pike. On the one hand, natural selection consistently *acted against* small pike. On the other hand, fishery selection consistently *favoured* small pike. Moreover, non-linear natural selection was often *stabilizing*, suggesting that bigger is not always better in pike (Fig. 1). In contrast, non-linear fishery selection was often *disruptive*, suggesting that the largest individuals were often not captured by the fishery (Fig. 3). By estimating the fitness function due to natural selection and fishery selection acting on Windermere pike within a given year, we evaluated whether year-specific selection pressures acted in concert or in opposition. These fitness functions corroborated the results of the traditional selection analyses by demonstrating that natural selection and fishery selection did indeed act in opposite directions in many years (Fig. 4). Finally, by comparing the fitness function based on natural selection alone to the total selection fitness function (natural selection × fishery selection), we found that the presence of opposing artificial selection has warped the fitness landscape, lowered the fitness function overall, and magnified the strength of stabilizing selection throughout the time series (Fig. 5).

We demonstrated that natural selection and harvest-induced selection oppose each other in a natural system, but how common is this result? Two key assumptions must be met for our results to hold true generally: (1) the two selective pressures must act in opposite directions and (2) the two selective pressures must be temporally consistent. This latter caveat might be true of selection imposed by harvest, particularly if harvest practices (e.g. season of harvest, mode of harvest, etc.) have been temporally consistent. However, recent evidence from long-term studies of natural selection in wild populations suggests that neither the strength nor the direction of natural selection can be assumed to be uniform (Grant & Grant 2002; McAdam & Boutin 2003; Carlson & Quinn 2007). For instance, work on the Darwin's finches (medium ground-finch, *Geospiza fortis* Gould) revealed that finches with large beaks were favoured after droughts when large, hard seeds were available whereas finches with small beaks were favoured after wet years when small, soft seeds were abundant (Grant & Grant 2002). While the strength of natural selection acting on Windermere pike fluctuated somewhat over the time series, the direction was remarkably consistent (Fig. 1): large fish were favoured over small fish (i.e. directional coefficients were positive), but the largest individuals sometimes suffered reduced survival (i.e. quadratic selection was stabilizing). Why might natural selection be so consistent in this system but not in others? Pike are cannibalistic (e.g. Grimm 1981; Persson *et al.* 2006), and so young pike are presumably under strong directional

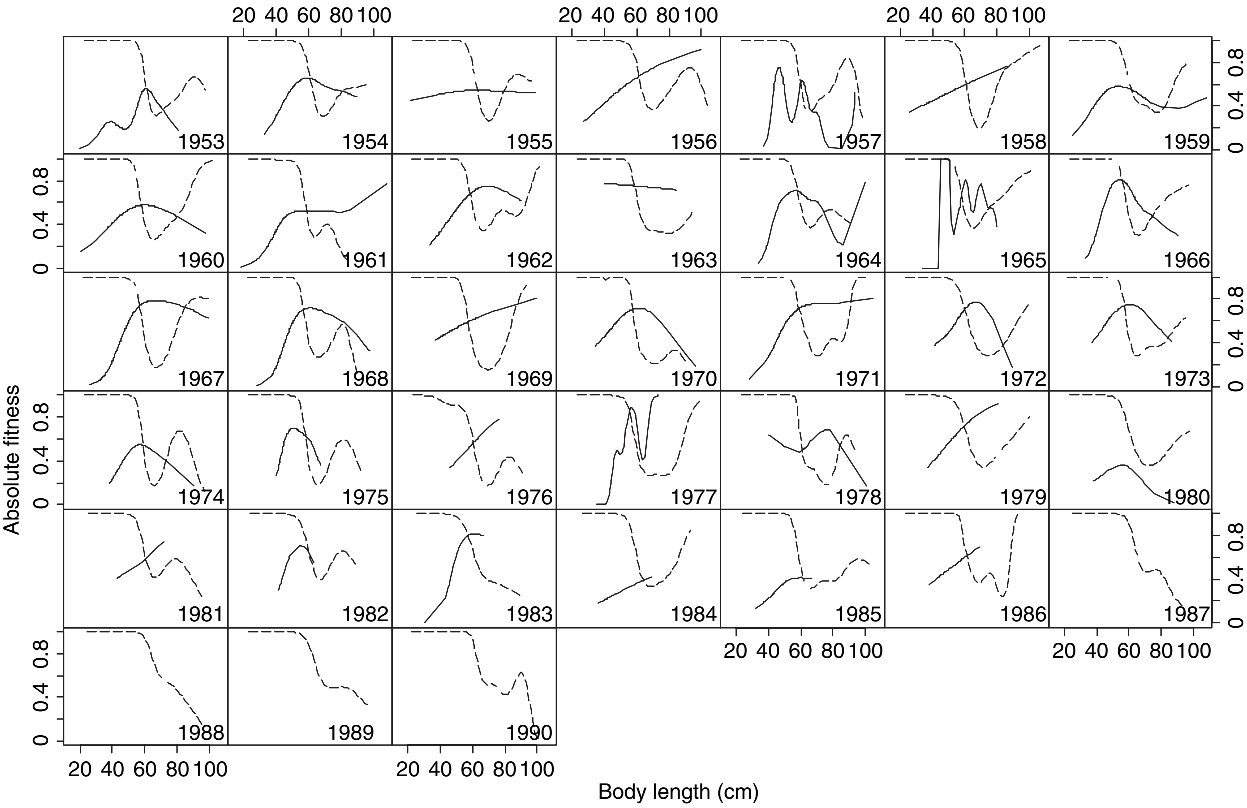

Figure 4 Relationship between pike body length and an individual's absolute fitness (0 = never recaptured and assumed dead; 1 = recaptured at a future sample/survived) partitioned by year (1953–1990). The solid line represents natural selection whereas the dashed line represents selection due to the fishery. In many years, individuals of intermediate lengths (*c.* 60 mm) had the highest fitness with regards to natural selection acting on pike body length. Fishery selection was often disruptive; individuals below *c.* 55 mm were not susceptible to the fishery whereas the largest individuals were vulnerable in some years (e.g. 1961, 1981, 1988, 1989) but not in other years (e.g. 1958, 1965, 1972, 1979, 1986). To visualize the total strength of fishery selection, we have included data from all fish in a single analysis (i.e. both sexes and all ages). Due to exceedingly small sample sizes for the natural selection analysis after 1986, only fishery selection results are presented for the period 1987–1990.

selection to grow quickly thereby minimizing the probability of being preyed upon by larger conspecifics. Moreover, Windermere is a temperate lake-system characterized by mild temperatures; i.e. it rarely froze over during the winter (only once since 1953) and summer water temperatures never exceeded 29°, the lethal temperature for pike (Bevelhimer *et al.* 1985; Windermere temperature data provided in Haugen *et al.* 2007) even in the face of recent warming of the lake (Winfield *et al.* 2004). Perhaps the relatively benign natural environmental conditions in Windermere explain the temporal consistency in the strength and direction of natural selection acting on pike body length. Thus, the answer to the question posed above likely depends on the degree to which selection pressures fluctuate temporally. We have provided an example in which the direction of both natural selection and fishery-induced selection fluctuated little, but this need not be the case.

Is human-induced selection impeding the natural adaptive process in Windermere pike? At the very least, fishery selection appears to be warping the fitness landscape relative to natural selection acting alone. In particular, a comparison of the natural selection fitness function and the total selection fitness function suggests that the addition of fishery-induced selection in this system has intensified the strength of stabilizing selection (Fig. 5) because fish longer than 55 cm suffer a fitness reduction due to the fishery. In many years, intermediate-sized pike enjoyed increased survival through the growing season only to be hit hardest by the fishery the following fall/winter (e.g. 1972, Fig. 4). What might be the consequence of such opposing selection on a self-sustaining population? On the one hand, factors that warp the adaptive landscape should promote the maintenance of naturally maladapted phenotypes, which could have ramifications on the long-term sustainability of the population. Indeed, Walsh *et al.*

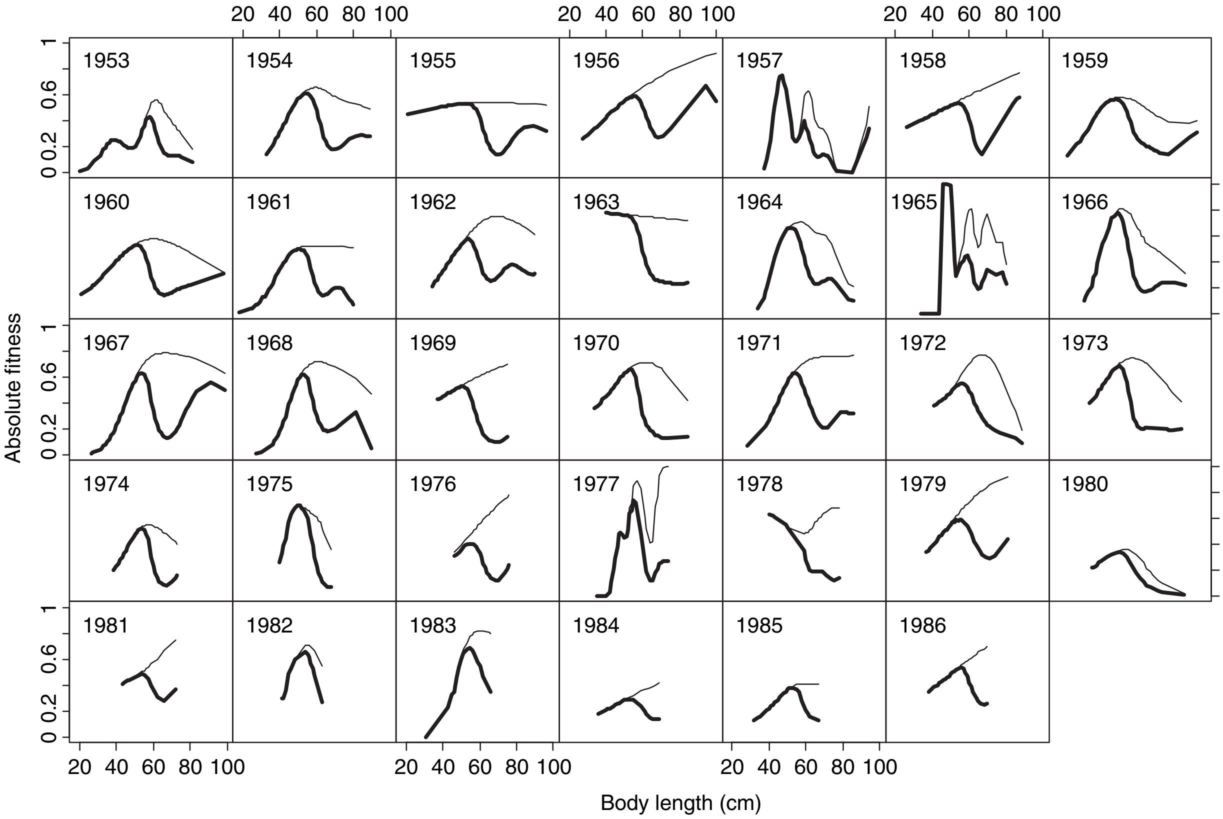

Figure 5 Relationship between pike body length and an individual's absolute fitness (0,1) partitioned by year (1953–1986). The bold line represents total selection (natural selection × fishery selection) and the thin line represents natural selection acting alone. Because individuals shorter than *c.* 55 cm were not targeted by the fishery, the two fitness functions show near perfect correspondence for small pike. Above 55 cm, the addition of fishery selection tends to decrease fitness overall relative to natural selection alone. Taken together, these results suggest that the addition of fishery-induced selection magnified the strength of stabilizing selection in this system.

(2006) demonstrate that maladaptive changes in a suite of traits correlated with body length (i.e. the trait being selected by the fishery) reduce the capacity for population recovery even after fishing effort has been markedly reduced. On the other hand, the response to selection (whether natural or human-induced) is adaptive and the population may have evolved in response to the anthropogenically altered adaptive landscape. Fisheries-induced adaptive changes have been reported in other systems (e.g. Sinclair *et al.* 2002; Barot *et al.* 2004; Olsen *et al.* 2004) and adaptive changes likely occurred in Windermere pike as well. Indeed, Edeline *et al.* (unpublished data) demonstrated that life-history traits of Windermere pike have evolved in the expected direction in response to dwindling fishing effort in recent years.

Reduced fishing effort in recent years (Fig. 2) should result in the emergence of a combined fitness surface that more closely resembles the fitness surface as determined by natural selection acting alone. Moreover, concomitant with a shift in the landscape, we would predict strong directional selection to push the population towards the newly emerging adaptive peak. Under this scenario, we would expect to see the strength of directional selection increase in parallel with the reduction in fishing effort but we did not (Fig. 1a). Rather, the strength of stabilizing selection increased through time (Fig. 1b). Theoretical predictions suggest that a population in evolutionary equilibrium will experience stabilizing selection around its mean whereas a population that has yet to attain equilibrium will experience directional selection pushing the trait mean towards the adaptive peak. This suggests that either Windermere pike quickly attained equilibrium after fishing effort dwindled in the 1970s or that the population's mean length under intensive fishery selection did not deviate substantially from the natural selection optimum length.

A reduction in fishing effort should also affect the strength and form of fishery selection. In particular, we would predict that the strength of selection due to the fishery would mirror the overall fishing effort. However, despite a marked reduction in fishing effort in recent years

(Fig. 2), the strength of selection due to the fishery has remained relatively constant over the time series (Fig. 3), and this result is consistent across ages and sexes. This suggests that despite a reduction in the number of fish captured, those fish that were caught at a younger age tended to be larger than fish caught at later ages.

Our results provide the first demonstration of opposing natural and human-induced selection in a natural system and a human-induced shift in the fitness landscape. Together these results suggest that harvest-induced selection hinders natural adaptive processes. The hypothesis that human impacts can smooth adaptive landscapes was advanced in one recent study (Hendry *et al.* 2006), and our results demonstrate the human-induced selection can also make the landscape more peaked because stabilizing selection was strengthened in the present study in response to harvest selection. The long-term ramifications of such anthropogenically altered landscapes are unknown but warrant further investigation.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Recapture probabilities and the importance of multiple recapture events.

- **Table S1** Using the Program MARK, we calculated the probability of recapturing an individual given that it was still alive (see Methods).
- **Figure S1** Cumulative number of recaptures as a proportion of the total recaptures from a given focal spring as a function of the relative recapture event.

Appendix S2 Year-specific results of the natural selection and fishery selection analyses.

- **Table S2** Natural selection summary (1953–1986).
- **Table S3** Fishery selection summary: age-3 females (fishery years: 1953–1990).
- **Table S4** Fishery selection summary: age-4 females (fishery years: 1953–1990).
- **Table S5** Fishery selection summary: age-4 males (fishery years: 1953–1990).
- **Table S6** Fishery selection summary: age-5 males (fishery years: 1953–1990).

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