The battle between harvest and natural selection creates small and shy fish

Christopher T. Monk[a,1], Dorte Bekkevold[b], Thomas Klefoth[c], Thilo Pagel[a], Miquel Palmer[d], and Robert Arlinghaus[a,e]

[a]Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany; [b]DTU Aqua, National Institute for Aquatic Resources, Technical University of Denmark, 2800 Kgs. Lyngby, Denmark; [c]Ecology and Conservation, Faculty of Nature and Engineering, City University of Applied Sciences, 28199 Bremen, Germany; [d]Department of Marine Ecology, Institut Mediterràni d'Estudis Avançats (Spanish National Research Council and Universitat de les Illes Balears), 07190 Esporles, Spain; and [e]Faculty of Life Sciences, Integrative Research Institute on Transformations of Human-Environment Systems, Humboldt-Universität zu Berlin, 10115 Berlin, Germany

Harvest of fish and wildlife, both commercial and recreational, is a selective force that can induce evolutionary changes to life history and behavior. Naturally selective forces may create countering selection pressures. Assessing natural fitness represents a considerable challenge in broadcast spawners. Thus, our understanding about the relative strength of natural and fisheries selection is slim. In the field, we compared the strength and shape of harvest selection to natural selection on body size over four years and behavior over one year in a natural population of a freshwater top predator, the northern pike (*Esox lucius*). Natural selection was approximated by relative reproductive success via parent–offspring genetic assignments over four years. Harvest selection was measured by comparing individuals susceptible to recreational angling with individuals never captured by this gear type. Individual behavior was measured by high-resolution acoustic telemetry. Harvest and natural size selection operated with equal strength but opposing directions, and harvest size selection was consistently negative in all study years. Harvest selection also had a substantial behavioral component independent of body length, while natural behavioral selection was not documented, suggesting the potential for directional harvest selection favoring inactive, timid fish. Simulations of the outcomes of different fishing regulations showed that traditional minimum size-based harvest limits are unlikely to counteract harvest selection without being completely restrictive. Our study suggests harvest selection may be inevitable and recreational fisheries may thus favor small, inactive, shy, and difficult-to-capture fish. Increasing fractions of shy fish in angling-exploited stocks would have consequences for stock assessment and all fisheries operating with hook and line.

boldness | reproductive fitness | harvest selection | telemetry | timidity

Anticipating and preparing for future evolutionary changes within harvested populations whether by fishing or hunting is critical for sustainable natural resource management and successful conservation of ecosystems (1–6). Harvest-induced evolution is a concern for both commercial and recreational fisheries, and harvest from recreational fisheries now frequently exceeds harvest from commercial fisheries in some marine fish and most inland fish populations (7). Harvesting, firstly, elevates adult mortality which favors the evolution of life history adaptations that maximize current as opposed to future reproduction [i.e., a fast life history characterized by early reproduction at a small size and elevated reproductive effort (1, 2)]. Additionally, harvesting is trait selective. Most individuals in harvested populations are not captured or hunted randomly (8). Instead, a suite of traits elevates the probability of harvest (8–13). In fisheries, vulnerability to harvest and fish body size are positively related across most fishing gears, and the relationship is exacerbated by the widespread use of minimum landing sizes (14, 15). Consequently, the average body size of individuals within fish stocks is commonly observed to decrease (15, 16).

Decreasing average body size in fish stocks first results from demographic truncation by direct removal of large individuals within a generation but may also result from evolutionary adaptation to a new fitness landscape (17). Positively size-selective harvesting alters the fitness landscape by favoring early reproduction at smaller sizes, in turn slowing down postmaturation growth due to altered allocation of energy from soma to gonads (2, 18). Additionally, reduced postmaturation growth may arise from evolutionary adaptations in energy acquisition–related behaviors [e.g., evolution of risk-sensitive foraging in response to the selective removal of bold, active, or aggressive behavioral phenotypes (19, 20)]. There is considerable debate whether any observed phenotypic changes, derived from monitoring data from wild fisheries, in life history traits such as maturation timing or growth rate are indeed evolutionary (i.e., genetic) or an effect of phenotypic plasticity (21), and a recent review concluded that no conclusive example for fisheries-induced evolution exists at the scale of wild fisheries (21).

Most research on fisheries-induced selection and evolution has been focused on life history traits (2). However, fisheries can also induce adaptive changes in behavior through at least two mechanisms. First, by creating selection pressures that favor fast life histories, fisheries may indirectly alter correlated behavioral traits like aggressive and bold behaviors (22–24). Second, passive

Significance

Fish are harvested nonrandomly, potentially inducing selection pressures and adaptations of phenotypes that could impede sustainable natural resource management. To assess the potential for fishing-induced selection, natural selection must also be considered, which represents a challenge in broadcast spawning fish in the wild. We compared harvest and natural selection on size and behavioral traits in a wild northern pike (*Esox lucius*) population. Harvest and natural selection on body size operated in opposition. Harvest but not natural selection acted directly on behavior, favoring timid fish. Simulations revealed fisheries selection on body size is likely not easily addressable using traditional length-based regulations and may thus be inevitable. Intensive recreational angling can therefore promote the development of small, inactive, shy, and difficult-to-capture fish.

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gear types such as gill nets, traps, or hooks heavily rely on a behavioral response by individual fish for successful capture (25). Fish that are able to forage more, at the expense of taking more risks, are able to grow faster and may produce more offspring (26–28), but they may also be more vulnerable to capture (10, 27) and mortality by predation (29). Accordingly, models comparing life history outcomes emerging from either purely behavioral to purely size-dependent vulnerability to capture demonstrate that behavioral selection can create the same pressures and ultimately evolutionary outcomes as size-selective capture and, depending on context, either favor bold or shy fish (30, 31). As personality traits are known to have a heritable component (32, 33) and vary consistently among individuals (34, 35), the selective capture of active, aggressive, and bold fish may ultimately promote the emergence of timid populations (10, 19, 27). Independent of life history adaptations, these changes may also disrupt the "pace-of-life" syndrome and the correlation of behavior and life history (24, 36, 37). A widespread increase in timidity implies that fish will become harder to catch (10). If this is the case, challenges in stock assessments will arise as they are built on assumptions of consistent fish availability to sampling gear over time to serve as indices of abundance (19, 38, 39).

Our understanding of selective harvest's impact on phenotypic change has not yet been able to fully explain empirical observations from fisheries in the wild (40, 41). Indeed, the rate and impacts of harvest-induced evolution continues to attract controversy despite more than 20 y of research (2, 21, 41). Models of harvest-induced life history evolution consistently underestimate rates of phenotypic change observed in empirical studies from the wild, while experimental studies in the laboratory tend to overestimate empirical rates of evolution (40–42). The discrepancy between models or laboratory studies and empirical data in the wild may partly result from plastic, rather than evolutionary, impacts on phenotypes collected in the wild (43), from inappropriate assumptions of fitness trade-offs in models (30, 31), from exaggerated fishing mortality induced in selection line experiments (44), or from inadvertent selection on other traits correlated with growth, such as behavioral traits, rather than direct selection on size (30, 31). To understand the potential for harvest-induced evolution, a key first step is to understand the selection pressures induced by exploitation in the wild (42, 45). This is because following the breeder's equation from quantitative genetics, the selection response in any trait is a product of the selection differentials acting on a trait and the trait's heritability (46). We focus here on estimating selection acting on adaptive traits in a wild fish population and compare the selection to natural selective forces on the same traits.

In particular, the counteracting forces of natural selection must be considered to understand the total selective forces acting on a phenotype (47, 48). However, natural selection has rarely been empirically measured in the context of harvest selection in wild fisheries (45, 47–49). Meta-analyses on selection in the wild indicate that fishing is one of the few anthropogenic selective forces consistently stronger than natural selection (49). Yet, natural selection compared to size-selective fisheries has, so far, only been quantified by fitness proxies such as survival (45), growth rate, or female body size (47, 48), assumed to be positively correlated with lifetime reproductive success (RS) (50). As the RS of fish is challenging to measure in the wild, it is unclear how body size and fitness actually scale (50), and consequently it is largely unclear what natural selection on body size or other traits looks like in exploited stocks. Further, the fitness landscape of behavioral traits has rarely been assessed in the wild, although behavior commonly relates to growth (51), survival (52, 53), and RS (26, 27).

Our aim was to quantify the strength and direction of harvest and natural selection in the wild using an experimentally exploited top predatory fish and to improve our understanding of whether a portion of harvest size selection is actually the result of undetected behavioral selection (54, 55). To that end, we investigated the strength and direction of harvest selection on body size and activity in northern pike, *Esox lucius*, measuring fitness in the context of natural selection as relative reproductive success (RRS) over four years and classification of movement behavior over one year using high-resolution acoustic telemetry (56) covering an entire natural ecosystem. We used hook and line fishing as an example of a widespread fishing gear used by both recreational and commercial fisheries. We predicted that harvest and natural size selection act in opposition in which larger fish would have higher RRS (50) but would also be more likely to be captured by angling (57, 58). Furthermore, we expected that fishing selection on size would be much stronger than natural selection (49). However, we also predicted additional harvest selection on behavior (55) because recreational fishing gear is known to be related to behavioral phenotypes (10, 55, 59–61). Finally, through simulations, we investigated how regulations could alter the relationship between harvest and natural selection and potentially counteract fishing selection considering minimum length limits and harvest slots based on established models (42).

Results

Pike Capture and Reproduction. In total, 806 adult pike were sampled by angling and electrofishing between November 28, 2007 and October 15, 2010, from a small, 25-ha mesotrophic natural lake in northeastern Germany. Of the 806 sampled adult pike, 430 individuals were captured at least once by angling using artificial lures while 376 fish were only sampled by electrofishing and assumed to be invulnerable to recreational angling gear. Of the 430 angled fish, 128 were also sampled by electrofishing. In total, we sampled 296 male pike (total length range: 20 to 59 cm, median: 37 cm) and 510 female pike (total length range: 23 to 87 cm, median: 46 cm), in which males were significantly smaller than females (t test, t = 12.818, df = 802.48, $P < 0.001$). Based on a mark-recapture–based population analysis, which estimated on average 1,844 (95% credible interval [CI] 1,601 to 2,061) individual pike age 1+ in the population and on average 838 (95% CI 719 to 940) fish in principle vulnerable to angling gear, we exerted an instantaneous recreational fishing mortality rate, F (per year), of 0.044 (95% CI 0.041 to 0.053), 0.22 (95% CI 0.21 to 0.25), 0.087 (95% CI 0.076 to 0.099), and 0.22 (95% CI 0.19 to 0.26) from 2007 to 2010, respectively (*SI Appendix*, Fig. S1). These values are consistent with fishing mortality rates from recreational pike fisheries which ranged from 0.04 to 0.22 (62). In our experiment we therefore induced practically realistic and generally moderate fishing mortality rates. Note that fishing mortality in our study means that we assumed theoretical harvest, as none of our fish were actually removed to be able to study reproductive fitness of individual fish repeatedly through several study years.

Using electrofishing and angling, we sampled 1,242 offspring from the 2007 through 2010 cohorts, including 712 age-zero juveniles, to measure individual RS as a natural fitness measure. We genetically assigned 804 offspring to adult pike (*SI Appendix*, Table S1), in which the number of offspring assigned also varied by cohort with 77, 311, 231, and 185 offspring assigned to either a mother, a father, or a parent pair in the 2007 through 2010 cohorts, respectively. The sampled offspring numbers included assignments based on pike captured in later years as adults (e.g., born 2007 and captured 2010) by angling or electrofishing. The inferred RS of adult pike was unequal, as 444 (55.1%) of the 806 adult pike never produced any sampled offspring. The average number of sampled offspring per adult with at least one offspring was 2.9 and 2.3 for females and males, respectively, and only 28 (3.5%) fish had six or more offspring in the sample including one fish which had 12 sampled offspring over four years (*SI Appendix*, Fig. S2).

We used high-resolution, whole-lake acoustic telemetry to assess the behavior of 50 individual pike (4 males and 46 females) over one year. The telemetry fish ranged from 34 to 80 cm total length (median: 55 cm total length). Over the tracking

period the average swimming distance per day ranged from 152 m to 3,823 m (median: 1,951 m). Fish size was positively correlated with activity (Pearson's product–moment correlation, t = 4.51, df = 48, $P < 0.001$, cor = 0.54).

Selection Gradient of Lande and Arnold. We applied the classic selection analysis of Lande and Arnold (63) to estimate linear (β_μ) and nonlinear (γ_μ) mean-standardized selection gradients (46) for natural and harvest size selection over four years of size selection and one year of behavioral (activity) selection for both sexes combined (refer to *SI Appendix*, Table S2 for sex-specific results). Fitness in the context of natural selection increased with increasing body size (Fig. 1) in which RRS was significantly related to size with a positive linear selection component and no nonlinear component (Table 1). By contrast, size was significantly related to angling vulnerability with a negative linear selection component and a disruptive nonlinear component, overall acting in opposition to natural selection on size (Table 1). Therefore, intermediately sized fish were the most vulnerable to harvest (Fig. 1), while the largest individuals had the largest reproductive output. When considering the subset of fish measured for activity in 2010, we detected no significant linear or nonlinear natural selection on size or activity; however, we found significant linear harvest-induced selection on both size and activity where larger and more active fish were more vulnerable to angling (Table 2). To parse the effect of size and behavior, we added activity (variance inflation factor = 1.4) to the harvest selection models and compared the outcome to the selection models with size alone. The addition of activity to the harvest selection models reduced the strength of size selection, but the mean standardized selection gradient for size remained larger than the mean standardized selection gradient for activity (Table 2). Accordingly, at the same size, a more active fish is more likely to be harvested than a less active one. Note that in our data set, pike length and activity were moderately correlated (Pearson correlation coefficient = 0.54). Thus, enough variance remained to estimate independent selection gradients on both length and pike activity in models in which both predictors were included (Table 2).

Distributional Selection Gradient. The classic Lande and Arnold (63) approach is well suited for assessing the shape and direction of selection, but the linear and nonlinear selection gradients cannot be combined to compare the overall strength of selection between natural and harvest selection. Therefore, we additionally quantified the distributional selection gradient (δ) which measures the absolute strength of selection independent of the shape or direction (64). Our estimation of δ agreed with the classic Lande and Arnold (63) assessment of selection. We found significant natural and harvest size selection (Table 1) in which harvest selection was slightly stronger than natural selection.

Table 1. Pike size selection

Selection type	β_μ (SE)	P	γ_μ (SE)	P	δ	P
Natural	0.781 (0.167)	<0.001	0.219 (0.235)	0.351	0.266	<0.001
Harvest	−0.534 (0.134)	<0.001	0.731 (0.219)	<0.001	0.410	<0.001

Linear mean standardized selection gradient ($\beta\mu$) estimates and their P values, nonlinear mean standardized selection gradient ($\gamma\mu$) estimates and their P values, and DSD distributional selection gradient (δ) estimates and their P values evaluated by permutation test for pike size selection in the context of natural and harvest selection.

When considering behavior and size selection jointly, our estimates of δ also found significant harvest selection on both size and activity (Fig. 2), but the overall strength of harvest selection was stronger on behavior than size compared to natural selection (Table 2). In fact, for the subset of fish with behavioral measures, no significant natural selection, according to δ, was found on size or activity (Table 2). Hence, harvest and natural size selection acted in opposite directions of nearly equal strength with a slight advantage to harvest selection. We did not find evidence for natural selection on behavior, suggesting fisheries were directionally favoring inactive fish.

Can Harvest Regulations Avoid Fisheries-Induced Selection? Simulating hypothetical regulations on top of our harvest data indicated that minimum length limits and harvest slots were only able to effectively mitigate the effects of size-selective harvest at very restrictive regulations (e.g., only harvesting pike > 70 cm). Initially, as the minimum length limit increased, we observed that the β_μ became slightly more negative; however, as the minimum length limit increased further, the β_μ reverted and began to approach zero (Fig. 3). The strength of selection, indicated by the distributional selection gradient δ, demonstrated the same pattern in which the strength of harvest selection increased with intermediate minimum length limits and began to approach irrelevance at high minimum length limits (Fig. 3). We observed that combining a maximum length limit and minimum length limit to produce a harvest slot dampened the effects of the minimum length limit but did not change the patterns observed simulating a minimum length limit alone (Fig. 3). For a given minimum length limit, a more restrictive maximum length limit in a harvest slot resulted in a reduction of size-selective harvest (Fig. 3). None of the regulations, except when overly restrictive leading to a total catch and release policy, avoided recreational fisheries selection altogether. Thus, we conclude that some degree of harvest selection on
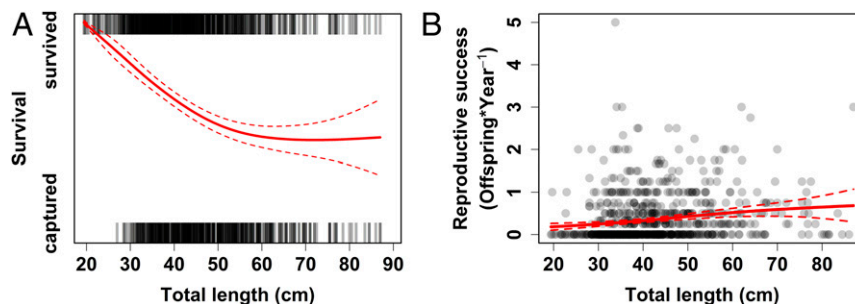

Fig. 1. Visualization of harvest and natural size selection. (*A*) Visualization of the shape of harvest size selection over four years of pike angling. The black marks show the raw capture data. Surviving fish were sampled by electrofishing but not by angling within a sampling season. The solid red line shows the shape of harvest size selection estimated by a generalized additive model (gam), and the dashed red lines show the 95% confidence interval of the gam. (*B*) Visualization of the shape of natural size selection of northern pike over four years of sampling. The raw RS data are shown by the black points, and the gam of RRS to show the shape of natural selection is shown by the solid red line. Dashed red lines show 95% confidence intervals estimated by a gam.

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Table 2. Pike behavior and size-selection over 1 year

Model	Selection type	Variable	β_μ (SE)	P	γ_μ (SE)	P	δ	P
Size alone	Natural	Size	−0.000756 (1.728)	0.999	9.593 (31.335)	0.760	2.626	0.929
	Harvest	Size	−0.782 (2.261)	0.00154	2.12 (40.535)	0.710	0.906	<0.001
Behavior and size	Natural	Size	1.306 (2.048)	0.527	11.726 (44.25)	0.792	2.117	0.928
		Activity	−1.176 (0.998)	0.244	−5.094 (7.974)	0.526	0.816	0.251
	Harvest	Size	−1.092 (2.754)	0.0422	−2.766 (85.704)	0.669	0.505	<0.001
		Activity	−0.368 (2.220)	0.0103	0.578 (18.889)	0.600	0.741	<0.001

Linear mean standardized selection gradient (β_μ) estimates and their P values, nonlinear mean standardized selection gradient (γ_μ) estimates and their P values, and DSD distributional selection gradient (δ) estimates and their P values evaluated by permutation test for pike size and activity selection in the context of natural and harvest selection. Model considering only size selection compared to models considering both size and behavioral selection indicate that a portion of size selection is attributed to behavioral selection, but size selection per se also occurs in addition to behavioral selection. Estimates are from for the subset ($n = 50$) of pike measured for behavioral traits using acoustic telemetry during one full year.

either size or behavior is inevitable in practical hook and line fisheries.

Discussion

The outcome of selective harvest can vary radically depending on the mechanisms driving selection (30, 31). A positively size-selective harvest may occur if large fish are disproportionally harvested either based on their size per se or because larger fish are behaving in a manner that increases their likelihood of capture. Our analysis of fishery selection on pike activity in nature suggests that a combination of both mechanisms is occurring. Despite pike activity and length being moderately correlated, we found independent harvest-induced selection on pike length and activity and the overall strength of behavioral selection to even be stronger than size selection in our case study involving hook and line fishing gear (55). Yet, because we only had behavioral data for one year and a reduced sample size, it is not yet clear whether behavioral selection has a counteracting natural selective that might have emerged in other years. In our single study year, behavioral natural selection was not present. Our findings that active fish are selectively captured by angling with no counteracting natural force support the hypothesis that passive fishing gear, such

as hook and line, may be promoting more timid (i.e., less active, aggressive, bold, and exploratory) traits within harvested pike populations (Movie S1) (19). Indeed, more active pike in the wild have been shown to be less active in an open field test, indicative of a coping style response (65, 66). Hence, more active pike are expected to belong to a proactive coping style demonstrating high aggression, low flexibility, and a low stress response (65). Our findings indicate the proactive pike types also selectively consume angling lures, inducing selection pressures toward reactive coping styles. It is therefore possible that such behavioral selection also affects underlying physiological traits (12, 67, 68).

We propose that sufficient evidence has accumulated, in addition to evidence from this study, that behavioral selection from passive fishing gears may be widespread (*SI Appendix*, Table S3), but this area of fisheries-induced selection is typically overlooked as researchers have overwhelmingly focused on life history adaptations to fishing (2, 9). In fact, as the counteracting natural selection pressure on behavior was not evident in our work, we expect particularly strong-angling fisheries-induced selection pressures acting on behavior that might outweigh the impacts on fish size selectivity. Clearly, our study has limits as it measures selection as opposed to evolutionary endpoints for one particular
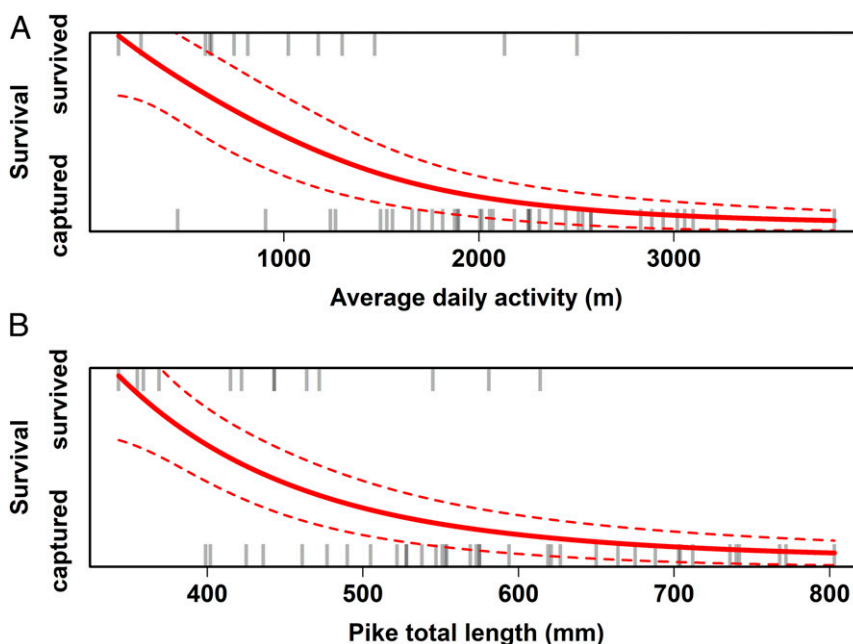

Fig. 2. Comparing size and behavior-selective harvest. Visualization of the shape of harvest selection on activity (*A*) and harvest selection on size for a subset of 50 pike (*B*). The black marks in *A* show the mean activity for each individual pike, and the black marks in *B* show the total length at tag implantation. Catch data are based on four years of sampling in which surviving fish were sampled by electrofishing but not by angling within the sampling year. The solid red line shows the shape of harvest selection estimated by a generalized additive model, and the dashed red lines show the 95% confidence interval each model.
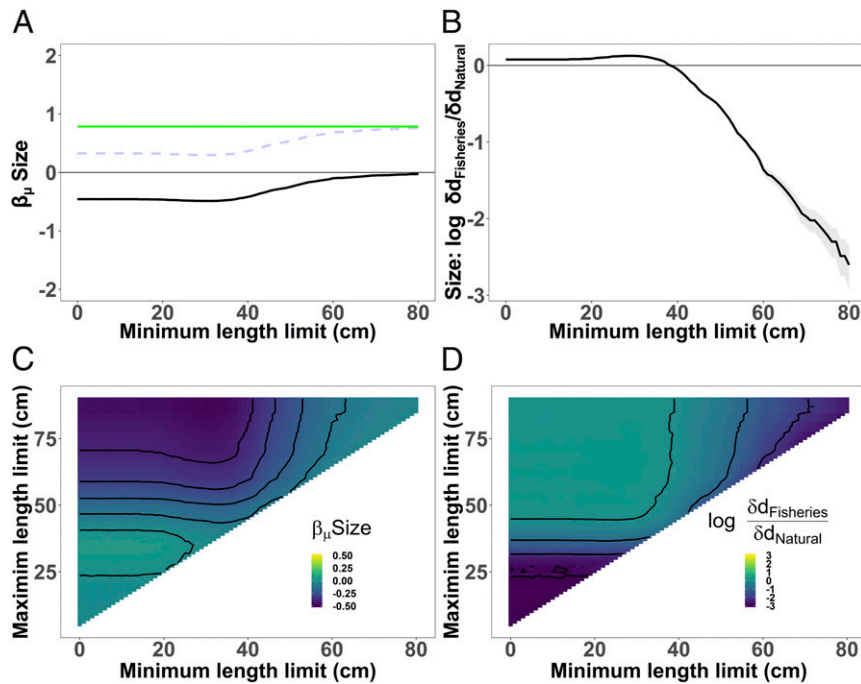
Fig. 3. Results of simulated minimum length limits and harvest slots on the balance between harvest and natural size selection. (*A*) The linear mean standardized selection gradient β_μ for harvest selection in black, natural selection in green (unaffected by simulations), and the total selection in blue (dashed). The total selection is the sum of the harvest and natural selection. (*B*) The ratio of strength or δ in log form between harvest and natural selection. If the ratio is above zero, harvest selection is stronger than natural selection, and if it is below zero, natural selection is stronger than harvest selection. (*C*) The linear mean standardized selection gradient β_μ for harvest selection given different combinations of minimum and maximum length limits. (*D*) The ratio of strength or δ in log form between harvest and natural selection given different combinations of minimum and maximum length limits. If the ratio is above zero, harvest selection is stronger than natural selection, and if it is below zero, natural selection is stronger than harvest selection.

passive gear type. Independent on any selection acting on behavior, one should generally expect adaptive changes toward a faster life history in response to multigenerationally elevated harvest as shown in a large body of both empirical and theoretical work (69–71). Our study adds to this knowledge by outlining the potential for strong selection on fish personality to happen in addition to life history selection when angling gear is involved.

We did not find a significant effect of natural selection on pike activity. However, our fitness estimate was based on a measure of RRS over four years while we only measured natural selection in relation to pike activity over one study year. By examining size selection on a yearly basis over four years, we found angling selection on size to be consistently present in the same direction in every year while natural selection was inconsistent, and in some years no natural selection on size could be detected (*SI Appendix*, Table S2). Only after aggregating four years of data to approach lifetime RS, the effect of natural selection on reproduction became visible. Accordingly, it is possible that natural selection acts also on pike activity, but we did not have sufficient sampling years to detect it. In general, our study represents a snapshot of potential long-term selection dynamics, and the long-term evolutionary outcomes of the trait selection we document remain unknown and can only be revealed by a multigeneration monitoring program (3, 72).

Any trait-selective harvest, regardless of how weak, will eventually cause evolutionary changes as long as the trait under selection has a heritable basis until the population achieves a new phenotypic equilibrium (73). The rate at which the population reaches such a new equilibrium will depend on the response to selection which is a product of the selection gradient and heritability (74). Hence, it should not be misconstrued that harvest and natural selection acting in opposite directions will cancel each other out and result in no changes in pike size. The correct interpretation of

our findings is that in our study system, the force of fishing selection negates the force of natural selection that would otherwise occur alone in an unfished state. That is, in the presence of fishing, the size of adult pike is expected to drop relative to the unfished state due to the consistently negative selection pressures caused by harvesting. If in addition, the life history also evolves earlier maturation or increased reproductive investment as multiple other studies suggest will happen (75, 76), the postmaturation growth decline might even be faster than suggested by our work (42).

Our analysis indicated that common harvest regulations in recreational fisheries, such as a minimum length limit or harvest slot, are likely unable to mitigate the effects of harvest-induced evolution but rather potentially enhance size-selective harvest at intermediate restrictions in agreement with previous findings (17, 42, 77). This is likely because at an intermediate minimum length limit, the difference in the chance of surviving a fishery by being small, compared to being large, is forcibly enhanced by regulations, elevating selection. At more restrictive regulations, in which the minimum length limit is increased, the effects of size-selective harvest begin to decline because the number of fish available to harvest (i.e., fishing mortality) must decline. Importantly, our simulations suggested that the harvest slot's maximum length limit did not alter the shape of selection but served to reduce fishing mortality relative to the minimum length limit alone, and therefore, adding a maximum length limit to a minimum length limit could slow rate of impacts from size-selective harvest (42, 78, 79). Regulations that directly limit fishing mortality such as harvest tags (80), caps on the angling licenses released, genetic management (81), or well-enforced and properly designed protected areas (33, 82) may therefore be the most effective at mitigating the impacts of selective harvest. Empirical data on the impact harvest regulations have on harvest selection from wild fisheries represents an important research frontier.

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Our aim was to quantify the effects of natural selection and harvest selection separately in the wild. Therefore, all harvested fish were released back into the experimental natural lake with the possibility to reproduce. Assuming that catch and release did not interfere with reproductive potential (83), we could therefore quantify natural selection under pristine unfished conditions. One downside to this approach is that density-dependent feedbacks were not present in the study system as in many laboratory-based fisheries-induced evolution studies (41). In real fisheries, the removal of large individuals in the lake will free up resources and can promote faster growth and earlier maturation of the unharvested individuals (84–86). Extra energy could increase the reproductive potential and fitness of those unharvested individuals, enhancing the differences between harvest and natural selection. Our results on the battle of natural and fisheries selection thus only hold for a pike stock at carrying capacity. These results will likely change as the fish can express phenotypic responses to reduced density as the fisheries are opened to real harvesting. In lakes with a long history of exploitation, the evolutionary relationships between growth and behavior may also be altered via fishing (36), possibly yielding a different balance between behavioral selection and size selection than we observed. This is a justification of further research. Before this research becomes available, our work suggests that recreational angling or other forms of hook and line fishing can counteract the natural selection for large body length and can increase the survival of timid fish that are harder to catch, which potentially can also have ecosystem effects (87, 88).

Conclusion

We conclude that fishery selection for fish inactivity (i.e., elevated timidity) as well as reduced natural selection on body size may be expected in an angler-exploited pike stock even at rather moderate fishing mortality rates. Our simulations suggest that such selection is unlikely to be avoided through simple harvest regulations unless these regulations are overly severe and approach a total catch and release policy. Because fishery stakeholders benefit from high vulnerability of fish to harvest by maintaining high catch rates, the reduced reactivity to fishing gear caused by fishery selection may have strong consequences for human well-being and affect stock assessments negatively (89). Additionally, alterations of fish behavior could have consequences for social groups, populations, and even food webs (19, 90, 91) that we can currently not properly estimate. Further research on this emerging topic is warranted.

Materials and Methods

Study Species. Northern pike was chosen as a study species for several reasons (92). First, several studies have previously compared harvest and natural selection in a well-characterized pike-population in England (47, 48), a population from which theoretical models have also been parameterized previously (42, 75). This allowed a good comparison of our results with previous studies and predictions. Second, the pike population in our study system, Kleiner Döllnsee (52◦59032.100 N, 13◦34046.500 E; Germany), has been well studied and characterized (51, 93–95), providing a more detailed context for our findings. Third, pike rarely live beyond 12 to 13 y in the wild (96) (the maximum age observed in Kleiner Döllnsee in this study was 12 y). Therefore, measuring RRS over four years as we did is a good approximation of lifetime fitness (97, 98). Fourth, pike are a highly valued fish species targeted across its circumpolar, northern hemisphere range by commercial and recreational fisheries (99, 100), and therefore, understanding the evolutionary dynamics of this species has the potential to support the management of an important fishery. In addition, northern pike is a widespread predatory species that occupies a broad range of aquatic environments (101).

Study Lake. Kleiner Döllnsee is a ∼25-ha (mean depth: 4.1 m; maximum depth: 7.8 m) dimictic, weakly eutrophic natural lake in Brandenburg, Germany, ∼80 km northeast of Berlin. The lake is a private research lake, closed to the public since 1992. The physical and biological attributes of the lake have been well characterized (83, 93, 102). The pike population in the lake can be considered natural with no known stocking activities. Further, the

natural inflow and outflow to the lake dried out in 1995, and therefore, the pike population was not connected to any other neighboring lakes during the study period of 2007 through 2010.

Fish Sampling. Adult and juvenile pike were sampled in the spring and autumn over four seasons. Adult pike were sampled by two methods, angling and electrofishing, while juvenile pike were sampled by electrofishing only. Fish were angled by very experienced pike fishers (usually members of our working group) using standard angling gear with free choice of lures. A battery-powered direct current electro-fishing unit (Type EFGI 4000, 4 KW, Brettschneider Spezialelektronik, Chemnitz, Germany, 40 cm–diameter ring anode) was used for electrofishing of the littoral zone. The accumulated angling effort over four years was 45.9 rod days. Electrofishing consisted of sampling the entire shoreline (2.2 km) on any given sampling day and occurred during 53 sampling events over the four-year sampling period.

Upon capture, each fish was anesthetized using a 9:1 95% EtOH:clove oil solution (Carl Roth, Karlsruhe, Germany) added at $1mL·L^{-1}$. Each fish above 15 cm total length was examined for a passive integrated transponder (PIT) tag (Trovan, Electronic Identification Systems, Germany) and identified using a handheld scanner (Trovan, Electronic Identification Systems, Germany). If no PIT tag was present, a new PIT tag was implanted in the dorsal musculature for future identification. The weight and total length of each pike was measured, and sex was determined by external examination of genital papilla following Casselmann (1974) (103). As sex determination for immature smaller fish was not always possible, sex was redetermined on future recaptures and corrected if necessary. Sex was later validated based on the size and age of the fish at capture. Seven to ten scales were removed dorsally just above the lateral line of each pike for aging and back-calculation of total length (104), and a fin clip was taken from the anal fin and preserved in ethanol to extract DNA for parental assignment. After sampling, all fish were released back into the lake. Handling mortality is extremely rare in pike (105, 106).

Growth. Sampled scales were mounted on glass slides, and the anterior distance from the scale origin to each annual growth mark was measured using the Quick Scope vision measurement device (Quick Scope Manual; Mitutoyo; https://www.mitutoyo.co.jp/eng/). At least three scales were read per individual pike, and pike were excluded when fewer than three readable scales were available.

Length-at-age was assumed to follow a Von Bertalanffy (VB) growth model at the individual fish level. The actual measurements of length-at-(re) capture(s) of any given fish were combined into a single integral model with the distance from the scale origin to each annual growth mark of the same fish. The relationship between fish length at capture to scale radius at capture was not linear and was modeled using a Gompertz model. The integral model was hierarchical in the sense that a growth curve has been fit to each individual pike and that the individual VB growth parameters were drawn from sex-specific distributions.

All the parameters of the integral model above have been estimated using a Bayesian approach implemented in a custom R script that runs Just Another Gibbs Sampler (JAGS) (19) for moving the Markov chain Monte Carlo (MCMC) chains. Prior distributions were uninformative. After reaching convergence, three chains were updated for 10,000 new iterations from which only one out of 100 iterations were kept for setting posterior distributions.

Parental Assignment. We used microsatellite markers at 16 loci to determine the parents of sampled offspring and adult pike as described in detail in previous publications (93). In brief, DNA was extracted from the fin clips using an E.Z.N.A. tissue DNA kit (Omega Bio-Tek, Inc.), and microsatellite loci were polymerase chain reaction (PCR) amplified and visualized using an ABI 3139 Genetic Analyzer (Applied Biosystems, Foster City, CA). Putative parent–offspring pairs were assigned using the CERVUS program version 3.0 (107). Parentage was assigned only when a genotype corresponded with that of a single parental candidate for at least 12 loci, using a 95% probability criterion (107). The probability of an offspring's father and mother being represented among parental genotypes was arbitrarily set at 80%. This was based on inference from mark-recapture analyses suggesting that relatively large proportions of the adult pike present in the lake in any given year had been sampled and genotyped. Whereas 80% may be slightly overestimating sampling efficiency (especially in the first year 2007), repeating analyses using lower values for this prior returned no differences in parentage assignments (107). In some cases in which multiple same-sex candidate parents showed no mismatch with an offspring, the parent with the highest log-likelihood score was assigned. Genotyping errors were estimated to be 0.02%. Parentage assignment analyses were carried out individually for the four years and parental candidates used in analyses differed

among sampling years to allow fish that were captured as juveniles in previous years to enter the pool of potential candidate parents in subsequent years after maturation.

Fish Maturity. Previous measurements of the pike population in Kleiner Döllnsee have indicated that the length at maturity for 100% of the population was 21 cm total length for males and 38 cm total length for females (108). Using parentage assignment, we found the smallest male-produced offspring with a spring size of 13 cm total length and a female-produced offspring at a spring size of 20 cm total length. Therefore, we assumed males above 13 cm total length and females above 20 cm total length could be mature and contribute to the next generation.

Fishing Mortality. To compare the findings of our study system with other fisheries and estimate the strength of fishing mortality that our experimental fishing exerted, we quantified the theoretical exploitation rate as fishing mortality imposed on the vulnerable study population. Instantaneous fishing mortality was quantified from the number of angled pike and the vulnerable population size.

Population size was estimated using a mark-recapture robust model (109). The sampling (angling and electrofishing) events were clustered into seven primary occasions (either spring or autumn; from 2007 to 2010) within which the population was considered closed. The analysis was restricted to fish one year-old or older (1+). Pike spawn in spring, and a given fish was assumed to enter to the population after the second spring. Instantaneous natural mortality of a given fish has been assumed to be length dependent (110). Estimates of fish-specific length-at-age along all its lifespan came from the output of the growth analysis described above. Between cohorts, differences in mortality were not considered. Detectability was assumed to be size dependent and modeled using a four-parameter Huisman–Olff–Fresco model (111). Size-dependent detectability was allowed to differ between angling and electrofishing.

The parameters of biological interest estimated by the mark-recapture robust model were 1) population size, 2) the sex- and age-dependent survival probability, and 3) the method- and size-dependent detectability. All parameters were estimated using a Bayesian approach implemented in a custom R script that runs JAGS (19) for moving the MCMC chains. As usual in Bayesian mark-recapture models, data augmentation (112) was implemented as a technical solution for dealing with the fact that population size is unknown. The maximum population size for the data augmentation approach was set to 7,344 fish (112). The Bayesian approach adopted here also allowed that the actual observed history of re-encounters for any given fish at the seven primary occasions considered can be enriched with data on the current state (death or alive) of the same fish coming from fish age (scales) and from parental assignment. Such an input enrichment was intended to improve the disentangling between detectability and mortality. Concerning parental assignment, it was ensured that the parents of any genotyped fish were alive at least at the corresponding spawning season even when they were never observed. Informative priors for mortality based on (110) were defined. The other prior distributions were uninformative or weakly informative. After reaching convergence, three chains were updated for 5,000 new iterations from which only one out five iterations were kept for setting posterior distributions. This model was run in a remote computation node and running last for 20.5 h.

Based on Arlinghaus et al. (75), we assumed a sigmoid relationship between length and the probability an individual is vulnerable to angling in which pike smaller than 20 cm were invulnerable and pike larger than 50 cm were fully vulnerable. We applied the sigmoid vulnerability function to the lengths of all individuals estimated by the mark-recapture model to determine each individual's probability of being vulnerable. For each fish in the population estimated by the mark-recapture model, we took a random draw from a binomial distribution based on the fish's probability of angling vulnerability to assign that individual as vulnerable (1) of invulnerable (0). The vulnerable population size was the count of vulnerable individuals. We repeated this process 10,000 times to attain a 95% confidence interval of the vulnerable population size. Fishing mortality F was then calculated by dividing the number of vulnerable individuals by the number of individuals harvested by angling in each sampling year.

Telemetry. We measured the behavior of a subset of 50 individual pike during 2010 using a high-resolution acoustic telemetry system that provides positional data for the entire lake at extremely accurate levels [see (102) for system details]. Combined radio and acoustic transmitters (Lotek Wireless, Newmarket, Ontario Canada; transmitter models: CH-TP-11–25, $n = 13$, dimensions = 11×65 mm, weight in water = 6.0 g; CH-TP-16–25, $n = 21$, dimensions = 16×55 mm, weight in water = 15.0 g; and CH-TP-16–33, $n = 16$,

dimensions = 16×63 mm, weight in water = 18.0 g) with burst rates of 9 s were surgically implanted into the body cavity of the focal 50 individuals (34 to 80 cm total length). Transmitter to body mass ratio was below 3.2%. Before surgeries, fish were anesthetized with a 9:1 95% EtOH:clove oil solution (Carl Roth, Karlsruhe, Germany) added at 1mL·L^{-1}, and transmitters were implanted according to methods described elsewhere (113, 114). We calculated several behaviors over 128 to 365 d (mean: 299 d) of tracking per individual during 2010. We summed the Euclidean distance between consecutive points to calculate the daily distance traveled, excluding distances below 5 m, the average error of the system (102). The daily distance traveled was averaged across the year to produce a measure of average activity for each pike. Previous work has shown that activity of pike in the lake is a repeatable trait and correlated to proactive behavioral types assessed under laboratory conditions (66).

Selection. Fitness was quantified in the context of harvest selection and natural selection. We estimated fitness to selection by angling because most pike fisheries in the temperate zone are recreationally exploited (115). Fitness was assigned a binary value in the context of harvest selection (0 if captured by angling and 1 if captured only by electrofishing). We released captured fish to give them an opportunity to reproduce and to measure their fitness in terms of natural selection; however, in our analysis of the data, we considered captured fish as (theoretically) harvested and therefore received a fitness of 0 in the context of harvest selection. To measure fitness in the context of natural selection, we calculated the RRS of each pike (116). RS, or the total number of offspring sampled, was standardized by the number of years a parent was mature in the sampling period. An individual pike's RS was divided by the mean RS in the population to obtain the RRS as is typical in selection studies (116, 117).

We used two complementary approaches to estimate harvest and natural selection. Firstly, we followed the classic Lande and Arnold (1983) (63) approach to estimate linear (correlational) and nonlinear (disruptive/stabilizing) selection components independently of mean standardized selection gradients (46, 74) by estimating regressions of fitness on traits such as body length or activity. Coefficients from nonlinear quadratic terms were doubled (118). Mean standardized selection gradients of natural selection were estimated using a linear regression as per 63; however, mean standardized gradients for harvest selection, which was a binary outcome, were estimated using a logistic regression and linearized as done in previous selection studies (45, 119). Significance of the mean standardized selection gradients was assigned based on an alpha level of 0.05. SEs of mean standardized selection gradients estimated by logistic regression were approximated by multiplying the SE from the logistic regression by the constant $1/\bar{W}$ in which $\bar{W}$ is mean fitness, as suggested by Janzen and Stern (119). We considered the total length at the time of capture as a measure of body size. We used the variance inflation factor to test for issues of multicollinearity between body size and activity, considering a variance inflation factor of three as an upper threshold (120).

We complemented the classic approach by calculating the distributional selection differential (DSD) gradient δ, which is a metric of the overall strength of selection robust to nonlinear selection components of any form (64). The DSD δ, however, does not indicate whether selection is in a positive or negative direction. Significance of δ was assessed by the permutation test described in (64). Further, we visualized the shape of selection with Generalized Additive Models [see (47), fit with the mgcv R package (121)] according to (117).

To assess whether error in offspring assignment could impact the conclusions of our selection analysis, we simulated scenarios in which a number of additional juveniles (1 to 5 juveniles per 50 parents, representing a high error rate) were randomly assigned to parents in addition to the assignments in our dataset. In total, 10,000 iterations were run in which offspring were randomly added to the dataset, RRS was recalculated, models were refit, and P values were retained. We then assessed whether the significance in our dataset agreed with the significance within the 0.025 and 0.975 quantiles of P values generated in the simulations (*SI Appendix*, Tables S4 and S5) and found that our conclusions remained robust.

Simulating the Selection Pressures with Harvest Regulations. Inspired by Matsumura et al. (42), we finally investigated the expected impacts of typical size-based harvest regulations on the battle between harvest and natural selection based on our empirical data. To that end, we tested a spectrum of minimum length limits from 0 cm to 80 cm in 1-cm increments and harvest slots (combination of minimum and maximum size limits) in which the maximum length limit varied from 5 cm above the minimum length limit (a very narrow slot) to 90 cm (a wide slot) and the minimum length limit varied from 0 cm to 85 cm in 1-cm increments. For each regulation tested, the fish in the empirical dataset that would be illegal to harvest according to the

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respective regulation were all given a fitness of 1 (survived the fishery) in the context of harvest selection. To simulate a very likely possibility of a small 5% discard mortality for protected fish (113), 5% of captured fish outside of a respective harvest limit were randomly reverted back to a fitness of zero. The mean standardized selection gradients and DSD δ for harvest selection were then recalculated for each regulation. Because of the stochasticity in the discard mortality, the simulation was repeated 10,000 times for the minimum length limits and 1,000 times for the harvest slots (due to long computing time), and the median, 0.025, and 0.975 quantiles were taken from the simulation results as the point estimate, upper, and lower confidence intervals, respectively.

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