

1 Thirty-five experimental fisheries reveal the
2 mechanisms of selection

3 Sébastien Nusslé^{1*}, Andrew P. Hendry², Roland A. Knapp³, Michael T. Bogan^{1,4}, Anna
4 M. Sturrock¹, & Stephanie M. Carlson¹

5

6 snussle@gmail.com

7

8 ¹Department of Environmental Science, Policy & Management, University of
9 California, Berkeley, CA, USA

10 ²Redpath Museum & Department of Biology, McGill University, Montreal, Quebec,
11 Canada

12 ³Sierra Nevada Aquatic Research Laboratory, University of California, Mammoth
13 Lakes, CA, USA

14 ⁴Current address: School of Natural Resources and the Environment, University of
15 Arizona, Tucson, AZ, USA

16

1 **Abstract**

2 Fisheries have been described as large-scale evolutionary experiments; yet such
3 “experiments” tend to be poorly replicated and therefore lack the predictive power
4 essential for designing appropriate management strategies to minimize the effects
5 of fisheries-induced selection. Large-scale removal of non-native trout from 35
6 montane lakes in California provided repeated experimental fisheries that allowed
7 us to explore how environmental parameters affect the three potential contributors
8 to overall selection: the fitness-trait correlation, trait variability, and fitness
9 variability. Our results demonstrate that fishing rapidly altered the size structure of
10 harvested populations, and that the magnitude of change was primarily driven by
11 the fitness-trait correlation (net selectivity). Fishing-induced selection was
12 repeatable overall but was also influenced by environmental (lake size and quality)
13 and demographic (size structure) parameters. Decomposing fishing-induced
14 selection into its key components can improve the management of stocks
15 experiencing fishing-induced selection by identifying the drivers of selection and
16 therefore the appropriate target for management.

17 **Text**

18 By targeting the oldest, largest, and most fecund individuals, size-selective fishing
19 can reduce recruitment and yield ^{1,2} and induce evolutionary changes that
20 negatively influence stock productivity, resiliency, and recovery ^{3,4}. However, two
21 major issues have hindered efforts to incorporate fishing-induced selection into

1 conservation plans and management strategies ⁵⁻⁷. First, studies of fishing-induced
2 selection are typically not well replicated within a species, and therefore lack the
3 potential to test for causal drivers through comparative analyses ⁸. Second, selection
4 can be shaped by three key components (the fitness-trait correlation, trait
5 variability, and fitness variability) ^{9,10} that have not been considered individually in
6 fisheries science, and yet have different implications for management (see below).
7 We circumvented these previous limitations through a study of fishing-induced
8 selection in 35 independent populations of fishes (brook trout, *Salvelinus fontinalis*;
9 and rainbow trout, *Oncorhynchus mykiss*).

10 The study populations were fished to extirpation through a large-scale non-native
11 fish removal as part of a habitat restoration and endangered species recovery
12 program in high elevation lakes of California's Sierra Nevada. Over 45,000 fish were
13 removed by means of gillnets and electrofishing, with length-at-capture and date-at-
14 capture recorded for nearly every captured fish ^{11,12}. After every fishing event, we
15 estimated the selection differential on fish length as the difference in the population
16 mean trait value before and after selection. This differential is equal to the
17 covariance between the trait and relative fitness ^{9,10}, which can be partitioned into
18 the product of three components: the correlation between the trait (body length)
19 and fitness (captured = 0, not-captured = 1), the variability (standard deviation) of
20 fitness, and the variability (standard deviation) of the trait. We then related among-
21 population variation in these components of selection to among-population
22 variation in lake physical characteristics (lake surface, maximum depth, elevation),
23 demographic (fish length, population size, density), fishing gear (gillnet,

1 electrofishing), and fishing intensity (proportion of the population captured,
2 number of fishing events, and time until extirpation) (see Extended Table 1).

3 Repeatable yet variable fishery selection

4 In most populations, the largest fish were quickly and consistently removed by
5 fishing, which dramatically altered the population size structure. Both mean fish
6 length and its variability decreased with increasing cumulative catch (Figure 1). On
7 average, fish length decreased by $-1.03 \text{ mm} \pm 0.13 \text{ mm (SD)}$ for each additional
8 percent of the population removed (i.e., “mm/%”; linear mixed regression: $t_{33.2} = -$
9 7.86 , $p < 0.001$). The average shift in mean length from the start to the end of the
10 fish removal period was $\sim 100 \text{ mm}$ (45% of initial mean body length). Fish length
11 variability (here measured as SD – similar results were obtained for CV) also
12 decreased with increasing cumulative catch: $0.32 \text{ mm} \pm 0.07 \text{ mm/\%}$ (linear mixed
13 regression: $t_{25.8} = -4.60$, $p < 0.001$). These estimates are conservative because the
14 mean duration of fish removal efforts was 2.5 years, during which time survivors
15 would continue to grow. With a moderate growth correction (5% per year, see
16 Methods), the estimates were $-1.11 \pm 0.13 \text{ mm/\%}$ for mean length (linear mixed
17 regression: $t_{33.4} = -8.68$, $p < 0.001$) and $-0.35 \pm 0.06 \text{ mm/\%}$ for variability in length
18 (linear mixed regression: $t_{25.3} = -5.4$, $p < 0.001$). With a larger – but still plausible –
19 growth correction (10% per year), the estimates were $1.18 \pm 0.13 \text{ mm/\%}$ for mean
20 length (linear mixed regression: $t_{33.2} = -9.37$, $p < 0.001$) and $-0.37 \pm 0.06 \text{ mm/\%}$ for
21 variability in length (linear mixed regression: $t_{25.1} = -6.06$, $p < 0.001$). These
22 decreases could not be explained by random harvesting because permutation

1 simulations, in which mortality was random, i.e., independent of fish length, yielded
2 non-significant slope coefficients for mean length (Figure 2a, one-sample t-test: $t_{99} =$
3 -1.173 , $p = 0.25$) and much lower slope coefficients for length variability (Figure 2b,
4 one-sample t-test: $t_{99} = -9.54$, $p < 0.01$).

5 The negative association between mean length and cumulative catch yielded
6 increasingly negative selection differentials (i.e., acting against large fish) with
7 increasing cumulative catch (Figure 3). Most differentials were negative (918 of
8 1092), with the few positive estimates tending to occur when precision was low (i.e.,
9 when few individuals remained in the population; Figure 3). The magnitude of the
10 selection differential increased with increasing cumulative catch: -0.31 ± 0.14
11 mm/% (mixed-model linear regression: $t_{30.2} = -2.20$, $p < 0.05$). As above, these
12 effects were even stronger when length was corrected for growth during the study
13 period: -0.35 ± 0.13 mm/% with a 5% correction (linear mixed regression: $t_{30.2} = -$
14 2.6 , $p < 0.05$); and -0.39 ± 0.12 mm/% with a 10% correction (linear mixed
15 regression: $t_{30.4} = -3.17$, $p < 0.01$). Importantly, even moderate fishing intensity (30-
16 40% of the population captured) led to selection differentials greater than 10 mm.
17 That is, fish surviving to that level of fishing were, on average, 10-20 mm (6-13%)
18 smaller than those in the original population (Figure 3). These estimates are similar
19 to other freshwater fish populations subject to low or moderate fishing intensity,
20 where selection differential estimates on individual growth tend to be 5-17%^{13,14}.

21 Among-population variability in selection differentials increased dramatically at
22 harvest levels above 80% (Figure 3). Indeed, modeling the distribution of selection

1 differentials after binning fishing intensity into 5% intervals revealed that the
2 variability of selection differentials (standard deviation within each 5% interval)
3 increased non-linearly with fishing pressure (quadratic, $R^2 = 0.62$, $F_{1,17} = 30.3$, $p <$
4 0.001). These results suggest that the outcome of size-selective fishing becomes
5 increasingly unpredictable when catch levels are high ($>80\%$), with some
6 populations exhibiting large decreases in mean length and other populations not
7 responding or even exhibiting increases in mean length.

8 These results confirm that fishing-induced selection can modify population size
9 structure, even at low fishing pressures. More importantly, these results also
10 highlight how the consequences of selection can be highly variable among replicate
11 populations. This unpredictability could explain some of the contradictory results of
12 fishing-induced selection reported in the literature ⁴. Moreover, our result that size-
13 selective fishing becomes increasingly unpredictable with higher fishing intensity
14 provides further evidence that reducing total harvest might be the best action to
15 recover severely impacted populations ¹⁵.

16 **Multiple factors mediate fishery selection**

17 The outcomes of fishing-induced selection differed among populations, which
18 provided an opportunity to explore the relative importance of the three components
19 of selection and examine how each was affected by environmental or demographic
20 attributes, or the fishing regime.

1 One component of selection is the correlation between the trait and fitness, in our
2 case represented by the selectivity of the fishing gear. Our results suggest that this
3 correlation is the most important component of selection in our system, accounting
4 for 60.9% of the variance in selection differentials (linear regression: $F_{1,33} = 51.5$, $p <$
5 0.001 , Figure 4). Variation among populations in this correlation, and hence
6 selection differentials, could be explained by several factors. First, correlations
7 between length and fitness were stronger in populations with initially smaller fish
8 (proportion of variance (PoVE) in the correlation explained by mean fish length:
9 29.6%, $F_{1,33} = 13.9$, $p < 0.001$). Second, correlations were stronger in populations
10 with higher densities (PoVE = 14.7%, $F_{1,33} = 5.68$, $p < 0.05$). Third, correlations were
11 weaker when the lake had at least one tributary (PoVE = 11.6%, $F_{1,33} = 4.34$, $p <$
12 0.05). These associations indicate that in a closed environment with many relatively
13 small fish, relatively large fish are more likely to be caught earlier. This suggests that
14 the selectivity of fishing gear (i.e., the strongest selective force) is highly influenced
15 by the environment. Indeed, a multiple regression including all three parameters
16 (fish length, density, and tributary presence) explained 47.6% of the variance in
17 correlation between trait and fitness (Figure 4).

18 Another component of selection is variability of the trait (i.e., size), which here
19 accounted for 21.1% of the variance in selection among populations ($F_{1,33} = 8.86$, $p <$
20 0.01 , Figure 4). Here too the environment played a role; length was more variable in
21 populations at lower elevations (PoVE = 18.8%, $F_{1,33} = 7.63$, $p < 0.01$) and in larger
22 lakes (PoVE = 15.2%, $F_{1,33} = 5.93$, $p < 0.05$). These results imply that, in our system,
23 lakes with greater habitat suitability (i.e., lower elevations are associated with

1 warmer temperatures and a longer ice-free season ¹⁶) and complexity (i.e., larger
2 systems tend to exhibit more complex habitat structure ¹⁷) support a more diverse
3 size structure, which makes them more susceptible to selection. This result might
4 provide insight into conflicting results in the literature, where some ^{13,14} – but not all
5 ¹⁸ – studies report strong selection against large fish in heavily-fished populations.
6 That is, even strong gear selectivity can yield only weak selection if trait variability
7 is already low – a hypothesis that would be easy to test in ongoing fisheries.

8 The last component of selection is variability in fitness, which here accounted for
9 29.3% of the among-population variance in selection ($F_{1,33} = 13.7$, $p < 0.001$, Figure
10 4), with populations experiencing evenly-distributed fishing events throughout the
11 study being less susceptible to fishery selection. In our study system, fitness
12 variability is indeed directly linked to the fishing regime, with populations
13 experiencing constant (even) fishing mortality throughout the season exhibiting
14 lower fitness variability than populations subjected to sporadic (uneven) fishing
15 events (see Extended Figure 1). This final component was not obviously linked to
16 any environmental factors; yet it was the only factor that differed between species,
17 with rainbow trout exhibiting slightly lower fitness variability than brook trout
18 (PoVE = 15.1%, $F_{1,33} = 5.85$, $p < 0.05$), potentially due to species-specific behavior
19 around fishing gears ^{19,20}.

20 Management Implications

21 Decomposing selection into its three components provides an opportunity to
22 identify the most important component of selection and, simultaneously, the

1 appropriate target for management. Our results suggest that overall selection can be
2 influenced differentially by each of the three selection components, each associated
3 with different management strategies to reduce the unintended consequences of
4 fishing-induced selection. In our particular system, even with gear that is
5 substantially less selective than those used in modern-day fisheries ^{21,22}, the most
6 important factor influencing the strength of fishing-induced selection was the
7 correlation between fitness and length, i.e., the fishing gear selectivity. In order to
8 manage populations against the potentially negative effect of size-selective fishing,
9 managers could introduce fishing gear regulations such as population-specific mesh
10 combinations protecting the largest individuals ^{23,24}. In addition, our data suggest
11 that tributaries entering lakes may provide some protection against size-selective
12 fishing. Tributaries may provide refuge for larger fish (i.e., a “reduced take zone”)
13 that decreases susceptibility to size-selective fishing. This supports the argument
14 that reserves provide an important management tool to mitigate fishing-induced
15 selection for populations in which selection is mostly driven by fishing gear
16 selectivity ²⁵⁻²⁸.

17 Alternatively, in populations where selection is mostly driven by trait variability,
18 management measures could focus on increasing the variability in fish length
19 through the protection of larger fish. Our results further suggest that environmental
20 characteristics such as habitat suitability and diversity also influence trait
21 variability, suggesting that habitat restoration activities could be implemented as an
22 indirect path to promoting trait variability ²⁹.

1 Finally, where selection is driven by fitness variability, management measures that
2 target fishing schedules and intensity (e.g., duration of the fishing season, daily
3 yield) could be effective strategies for reducing fishing-induced selection. Our
4 results suggest that fitness variability is directly linked to the fishing schedule (see
5 Extended Figure 1), with even fishing throughout the season being less selective
6 than infrequent, but intense, fishing events ³⁰.

7 These findings also highlight an interesting feedback that might shape fisheries-
8 induced selection, and our ability to detect it. In particular, strong size-selectivity of
9 fishing gear imposes substantial selection on body size in harvested fishes. At the
10 same time, however, this selectivity should decrease size (and fitness) variability,
11 which should reduce the intensity of selection. Therefore, we have a situation where
12 selection differentials might decrease through time in harvested populations even if
13 gear selectivity itself is constant. Stated more generally, selection differentials might
14 not be good indicators of gear selectivity, and investigating how the different
15 components of selection vary through time might be necessary to assess how size-
16 selective fishing has impacted populations.

17 Conclusions

18 Our study helps explain why the outcomes of fishing-induced selection reported in
19 the literature are contradictory ⁴. First, size-selective fishing becomes increasingly
20 unpredictable with higher fishing intensity. Second, responses to fishery selection
21 are population-specific because fishery selection is influenced by demographic- and
22 habitat-specific factors. Predicting population responses to fishing-induced selection

1 is a key challenge faced by fishery managers ³¹⁻³³, but it has been overshadowed by
2 controversy surrounding its effects and underlying mechanisms ^{34,35}. By working
3 with replicated populations, we were able to explore practical principles of fishing-
4 induced selection that could help guide management of harvested stocks. Most
5 importantly, evolutionary impact assessments ³¹ should replicate selection
6 measures at the subpopulation level to investigate the repeatability of selection
7 across time and space. Doing so will enable managers to disentangle the
8 components of selection and to tailor their management actions accordingly.

9 Overall, our study demonstrates that fishing is highly selective, even at low harvest
10 rates. As size-related traits are heritable ³⁶, this selection has the potential to
11 dramatically modify both the size and genetic structures of harvested populations.
12 However, the outcomes of selection are highly variable and can be modified by
13 environmental, demographic- and species-specific factors. Disentangling these
14 factors and the different components of selection (fitness-trait correlation, trait
15 variability, fitness variability) is critical to producing flexible and relevant
16 management strategies, but does rely on repeated measurements of selection.
17 However, such experiments may not need vast numbers of individuals because our
18 results suggest that selection differentials varied linearly with catch. Evolutionary
19 impact assessments that incorporate these components of selection will allow
20 managers to predict how a population will respond to different harvest rates and
21 management scenarios with far greater accuracy than is currently achieved.

1 **Methods**

2 Study system: large-scale experimental fisheries

3 The Sierra Nevada mountain range contains thousands of lakes that are naturally
4 fishless above 1800 meters ³⁷. Most of these lakes have been stocked with non-
5 native trout, some as early as 1850, to create recreational fishing opportunities ³⁸.
6 By 1996, 63% of the lakes larger than one hectare were inhabited by non-native
7 populations of rainbow trout (including hybrids with golden trout) and/or brook
8 trout ³⁸. In the past 20 years, research has revealed detrimental effects of non-native
9 fish on native biota, particularly endemic mountain yellow-legged frogs (*Rana*
10 *muscosa* and *R. sierrae*) ^{11,16,39}. Consequently, several large-scale fish removal
11 programs were initiated in Inyo National Forest and in Sequoia, Kings Canyon, and
12 Yosemite National Parks. These programs involved sinking multimesh (six panels,
13 each with a different mesh size from 10-38 mm) gillnets (86% of all captures) and
14 performing electrofishing on lake shores and inlet and outlet streams (14%) ¹¹. The
15 multimesh nets are designed to target fish across the full range of sizes and ages,
16 and are generally considered less selective than traditional fishing gear ^{23,40}.

17 To date, fish have been completely removed from over 60 locations (lakes and
18 rivers); and from these, we analyzed lake populations where at least 15 fish were
19 captured over at least three fishing events. This reduced dataset included 35
20 populations from 32 lakes: 17 lakes with rainbow trout, 12 lakes with brook trout,
21 and three lakes with both species. The number of fish removed per lake ranged from

1 19 to 4741 over 29 to 3307 days (Extended Table 1). A total of 47,679 fish were
2 caught and the total length-at-capture (mm) and date-at-capture were recorded.
3 The dataset includes almost all the fish present in each lake, excluding only fish that
4 died from natural mortality during the removal period.

5 The 32 lakes exhibited large variability in environmental and population-specific
6 parameters (Extended Table 1). Lake size was indexed as lake perimeter (207-2118
7 m), lake area (1989-124625 m²), and maximum depth (2.5-30 m). Lake quality (i.e.,
8 the potential for rapid fish growth) was indexed as elevation (2146-3583 m; lower
9 elevations assumed to represent higher quality habitat ¹⁶) and maximum fish length
10 (200-550 mm). Population size structure was indexed as mean fish length (range
11 among lakes: 93-347 mm) and length variability (standard deviation; range among
12 lakes: 27-94 mm). Lakes also differed in population size (19-4741 individuals),
13 density (5-3355 individuals per ha), and various aspect of the fishing regime,
14 including the proportion of fish caught with gillnets (28-100%) versus
15 electrofishing, the number of fishing events (5-114 events), and the mean number of
16 fish caught per event (2-145 fish per event) or per day during the overall study
17 duration (0.05-6.9 fish per day).

18 Catch and length

19 We assessed the selective effect of fishing by correlating fish length with catch
20 intensity. Specifically, after every fishing event, we assigned to each fish a catch
21 intensity value equal to the number of fish caught to date, divided by the total
22 number of fish in the lake (i.e., the proportion of fish captured to date). We then

1 assessed the relationship between catch intensity and length-at-capture by means of
2 linear mixed-models; these models included length-at-capture as response variable,
3 catch intensity and species as a fixed effects, and lake ID as a random effect, allowing
4 the slope and intercept to vary among lakes. We used the same type of model to
5 assess the effect of fishing intensity on the variability of length-at-capture, which
6 was measured after each fishing event, as the standard deviation of the length of all
7 the fish remaining in the lake. Analyses were performed using both linear and
8 logarithmic relationships, as changes over time might not be linear. The linear
9 model had the better fit and so was used in all analyses presented herein. Because
10 no differences emerged between the two species (rainbow trout and brook trout),
11 we pooled species for all analyses presented here (Figure 1); we tested for species
12 effects when analyzing the component of selection (see below and Figure 4).

13 For the sake of simplicity, we first assumed that fish did not grow during the study
14 period (typically 2-3 years), which would result in a conservative (underestimated)
15 estimate of selection. This simplification is reasonable given that fish growth is
16 extremely low in these high elevation lakes due to low temperatures and
17 productivity, as well as the short growing season ¹⁶. However, to examine the
18 sensitivity of our results to growth, we next adjusted the observed length-at-capture
19 at a given capture date by expected growth rate since the start of the experimental
20 fisheries. To do so, we applied two growth scenarios: a slow growth correction
21 assuming 5% length increase per year and a fast growth correction assuming 10%
22 length increase per year. With this method, the length of the fish captured during

1 the course of removal was adjusted to their expected length at the first date of
2 sampling after allowing for growth.

3 To test if random sampling could explain the observed selective effects of fishing -
4 estimated as the slopes of the length-catch intensity relationships (Figure 1a), and
5 variability-catch intensity relationships (Figure 1b) - we performed 100 simulations
6 where mortality occurred randomly; i.e., we used random permutations of the time-
7 at-capture of each fish. We performed the same tests (linear mixed models) on the
8 random simulations, allowing direct comparison of the observed and simulated
9 data. For each simulation, we extracted the slope of the relationship between length-
10 at-capture (or length variability) and catch intensity, in order to build an empirical
11 distribution of the expected change in length (and variability) with catch. We
12 assumed that these distributions were normally distributed, estimated their means
13 and standard deviations, and tested if the expected change (based on the mean of
14 the distributions) differed from zero with one-sample t-tests (Figure 2).

15 When possible, fish were prevented from reaching spawning areas in the associated
16 streams by makeshift dams and/or gillnets to block access to inlet and outlet
17 streams. In addition, efforts were made to reduce reproduction during the
18 experimental fisheries, by searching for and destroying redds (groups of fertilized
19 eggs buried in spawning grounds). However, some reproduction cannot be
20 completely ruled out after the initiation of the experimental fisheries, in particular
21 for brook trout that are known to breed in lake habitat ⁴¹. If any reproduction
22 occurred, it likely occurred during the first year following removal initiation and

1 likely produced few fish as most adults were removed quickly. To estimate the
2 potential effect of reproduction after the initiation of the fisheries, we performed a
3 sensitivity analysis by repeating the analysis after removing fish smaller than 50
4 mm that were caught after the first year of survey, i.e., 334 fish potentially born after
5 removal initiation. This is a conservative correction, as we also removed all the
6 smaller fish born before the start of the study. Re-analyzing the data using this
7 reduced dataset, the results were nearly identical, with a corrected relationship
8 between length and catch of -97.7 ± 13.1 [***], i.e., a 5% difference, which is less
9 than the difference with moderate growth correction (see above). The corrected
10 relationship between variability and catch was -0.34 ± 0.06 [***], and the corrected
11 relationship between selection differential and catch was -0.34 ± 0.15 [*], see Fig. 1
12 & 3 for the reported impact. Thus, fishing-induced selection appears to be driven by
13 the removal of the largest fish, and the effects of potential reproduction during the
14 program were deemed to be negligible.

15 Estimating selection differentials

16 For each lake, we compared the mean length of surviving fish after each fishing
17 event (1092 events) to the mean length before the same fishing event, yielding a
18 selection differential for each event in each lake. Under several common
19 assumptions, this differential is equal to the covariance between trait and relative
20 fitness¹⁰. Using this covariance, we can disentangle the different components of
21 selection into the products of (1) the correlation between the trait and fitness, (2)

1 the variability (standard deviation) of fitness, and (3) the variability of the trait
2 under selection (see below) ¹⁰.

3 Selection differential: $\bar{Z}^* - \bar{Z} = cov(W, Z) = cor(W, Z)\sigma_W\sigma_Z$

4 With \bar{Z} the average value of the trait Z in the population (in this study Z is the length
5 of the fish), \bar{Z}^* the average value of the trait Z after selection, i.e., in the sub-
6 population that survived the harvest event, W the relative fitness, σ_W , the standard
7 deviation of the relative fitness, and σ_Z the standard deviation of the length in the
8 initial population.

9 We evaluated fishing-induced selection by correlating selection differentials with
10 catch intensity. Specifically, for each lake we compared the selection differential
11 generated by each fishing event to the proportion of fish captured to date (i.e., the
12 catch intensity, described above). We then assessed the relationship between
13 selection differentials and catch intensity by means of linear mixed-models; these
14 models included selection differentials as the response variable, catch intensity as a
15 fixed effect, and lake ID as a random effect, allowing the slope and intercept to vary
16 among lakes (Figure 3a).

17 To assess if catch intensity also affected the variability in selection differentials, we
18 binned catch intensity into 5% intervals and estimated, for each lake, the average
19 selection differential in each 5% interval. For example, to estimate the average
20 selection differential in the 15-20% interval, we averaged - for each lake - all the
21 selection differential estimations with catch intensity being within this interval.

1 Then we measured the between lake variability within each interval as the standard
2 deviation of the averaged selection differentials. Since there is only one value per
3 catch interval, we used linear models to assess how the variability in selection
4 differentials was affected by catch intensity (Figure 3b).

5 Selection differential components and environmental parameters

6 In each lake and after each fishing event, we estimated the three components of
7 selection. Specifically, after each fishing event, fish that had been captured were
8 assigned a fitness value of zero, and one if not captured. This allowed estimating (1)
9 the correlation between body length and fitness, the standard deviation of fitness
10 (σ_W), and the standard deviation in body length before selection (σ_Z) in each lake
11 and after every fishing event. To allow for between-lake comparisons and to
12 estimate the effect of attributes related to the environment, fish population, or the
13 fishing regime, we calculated, for each selection component, a single estimate per
14 lake. For the covariance and the correlation between fitness and trait, we used the
15 mean value of all estimates (calculated after every fishing event). To estimate the
16 standard deviation in fitness in each lake (σ_W), we used the standard deviation of all
17 individuals' relative time-at-capture (as a proportion of the population captured).
18 Specifically, within each lake, we transformed the time-at-capture into a [0,1]
19 variable, with zero being assigned to the fish caught during the first fishing event,
20 and one assigned to the fish caught during the last fishing event. This value
21 represents how spread the fishing events are throughout the study duration, and is
22 minimal when several fishing events are distributed evenly throughout the study

1 and maximal when few fishing events are distributed at the beginning and the end
2 of the study (see Extended Figure 1). We then estimated the standard deviation in
3 body length before selection (σ_Z). Finally, because the selection differential is the
4 covariance between fitness and trait, and is mathematically linked to the three
5 components of selection components¹⁰, we calculated an independent value for the
6 selection differential. Instead of the covariance between fitness and trait, we used
7 the relationship between catch and length-at-capture (see Figure 1a) as a proxy for
8 overall selection. This value represents the magnitude of length change when catch
9 increases and can be understood as fishing-induced selection. We assessed the
10 validity of this proxy with a linear regression between the slope of the length-catch
11 relationship and the covariance between length and fitness (linear regression: $F_{1,33} =$
12 14.3 , $p < 0.001$, $R^2 = 0.30$).

13 Finally, we assessed the contribution of each selection component to overall
14 selection by means of weighted analysis of variance. Specifically, overall selection
15 was the response variable, the three components of selection were predictor
16 variables (Figure 4), and the logarithm of population size was the weighting
17 parameter. We used one-way analysis of variance for each individual component,
18 but also checked the additive effects of selection components with multiple
19 regression. Finally, we assessed the contribution of the environmental and
20 population-specific variables (lake size, lake quality, population structure,
21 population size, and fishing regime) to each selection component by means of
22 stepwise linear regression and weighted analysis of variance as before.

1 **Data and statistics**

2 The data that support the findings of this study belong to the National Park Service
3 and the California Department of Fish and Wildlife, and can be accessed through
4 them upon reasonable request. The code used to generate results of this study is
5 available from the corresponding author upon request.

6 All analyses were performed in R ⁴². The exact sample size in each group is reported
7 in Extended Table 1, for both the number of individuals per lake (Pop. size) and for
8 the number of selection estimates generated after each fishing event (Number of
9 fishing events). Effects are reported as mean \pm standard deviation for linear models,
10 and percentage of variance for analyses of variance. All test are two-sided, and
11 reported with the value of the statistic and the degrees of freedom. Model
12 assumptions of residual normality were assessed visually with histograms. Mixed
13 models were fitted with the `lmer()` function from the package `lme4` ⁴³. Significance
14 tests were computed according to Kuznetsova et al. ⁴⁴ using the package `lmerTest`.

15

1 Bibliography

- 2 1. Hixon, M. A., Johnson, D. W. & Sogard, S. M. BOFFFFs: on the importance of
3 conserving old-growth age structure in fishery populations. *Ices J. Mar. Sci.* **71**,
4 2171–2185 (2013).
- 5 2. Birkeland, C. & Dayton, P. K. The importance in fishery management of leaving
6 the big ones. *Trends Ecol. Evol.* **20**, 356–358 (2005).
- 7 3. Conover, D. O. Fisheries - Nets versus nature. *Nature* **450**, 179–180 (2007).
- 8 4. Heino, M., Díaz Pauli, B. & Dieckmann, U. Fisheries-Induced Evolution. *Annu.*
9 *Rev. Ecol. Evol. Syst.* **46**, 461–480 (2015).
- 10 5. Borrell, B. Ocean conservation: A big fight over little fish. *Nature* **493**, 597–
11 598 (2013).
- 12 6. Smith, T. B. & Bernatchez, L. Evolutionary change in human-altered
13 environments. *Mol. Ecol.* **17**, 1–8 (2008).
- 14 7. Law, R. Fisheries-induced evolution: present status and future directions. *Mar.*
15 *Ecol. Prog. Ser.* **335**, 271–277 (2007).
- 16 8. Hutchings, J. A. & Fraser, D. J. The nature of fisheries- and farming-induced
17 evolution. *Mol. Ecol.* **17**, 294–313 (2008).
- 18 9. Brodie, E. D., III, Moore, A. J. & Janzen, F. J. Visualizing and quantifying natural
19 selection. *Trends Ecol. Evol.* **10**, 313–318 (1995).
- 20 10. Lande, R. & Arnold, S. J. The measurement of selection on correlated
21 characters. *Evolution* **37**, 1210–1226 (1983).
- 22 11. Vredenburg, V. T. Reversing introduced species effects: experimental removal

- 1 of introduced fish leads to rapid recovery of a declining frog. *Proc. Natl. Acad.*
2 *Sci. USA* **101**, 7646–7650 (2004).
- 3 12. Knapp, R. A. & Matthews, K. R. Non-native fish introductions and the decline of
4 the mountain yellow-legged frog from within protected areas. *Cons. Biol.* **14**,
5 428–438 (2001).
- 6 13. Nusslé, S., Brechon, A. & Wedekind, C. Change in individual growth rate and its
7 link to gill-net fishing in two sympatric whitefish species. *Evol. Ecol.* **25**, 681–
8 693 (2011).
- 9 14. Nusslé, S., Bornand, C. N. & Wedekind, C. Fishery-induced selection on an
10 Alpine whitefish: quantifying genetic and environmental effects on individual
11 growth rate. *Evol. Appl.* **2**, 200–208 (2009).
- 12 15. Kuparinen, A. & Merilä, J. Detecting and managing fisheries-induced evolution.
13 *Trends Ecol. Evol.* **22**, 652–659 (2007).
- 14 16. Knapp, R. A. & Dudley, T. L. Growth and longevity of golden trout,
15 *Oncorhynchus aguabonita*, in their native streams. *Calif. Fish Game* **76**, 161–
16 173 (1990).
- 17 17. Barbour, C. D. & Brown, J. H. Fish species diversity in lakes. *Am. Nat.* **108**, 473–
18 489 (1974).
- 19 18. Andersen, K. H. & Brander, K. M. Expected rate of fisheries-induced evolution
20 is slow. *Proc. Natl. Acad. Sci. USA* **106**, 11657–11660 (2009).
- 21 19. Biro, P. A. & Post, J. R. Rapid depletion of genotypes with fast growth and bold
22 personality traits from harvested fish populations. **105**, 2919–2922 (2008).
- 23 20. Biro, P. A. & Sampson, P. Fishing directly selects on growth rate via behaviour:

- 1 implications of growth-selection that is independent of size. *Proc. R. Soc. B*
2 **282**, 20142283 (2015).
- 3 21. Kuparinen, A., Kuikka, S. & Merilä, J. Estimating fisheries-induced selection:
4 traditional gear selectivity research meets fisheries-induced evolution. *Evol.*
5 *Appl.* **2**, 234–243 (2009).
- 6 22. Allendorf, F. W. & Hard, J. J. Human-induced evolution caused by unnatural
7 selection through harvest of wild animals. *Proc. Natl. Acad. Sci. USA* **106**,
8 9987–9994 (2009).
- 9 23. Jensen, J. W. Gillnet selectivity and the efficiency of alternative combinations
10 of mesh sizes for some freshwater fish. *J. Fish Biol.* **28**, 637–646 (1986).
- 11 24. Hutchings, J. A. Avoidance of fisheries-induced evolution: management
12 implications for catch selectivity and limit reference points. *Evol. Appl.* **2**, 324–
13 334 (2009).
- 14 25. Hilborn, R. *et al.* When can marine reserves improve fisheries management?
15 *Ocean Coast. Manage.* **47**, 197–205 (2004).
- 16 26. Baskett, M. L., Levin, S. A., Gaines, S. D. & Dushoff, J. Marine reserve design and
17 the evolution of size at maturation in harvested fish. *Ecol. Appl.* **15**, 882–901
18 (2005).
- 19 27. Dunlop, E. S., Baskett, M. L., Heino, M. & Dieckmann, U. Propensity of marine
20 reserves to reduce the evolutionary effects of fishing in a migratory species.
21 *Evol. Appl.* **2**, 371–393 (2009).
- 22 28. Baskett, M. L. & Barnett, L. The ecological and evolutionary consequences of
23 marine reserves. *Annu. Rev. Ecol. Evol. Syst.* (2015). doi:10.1146/annurev-

- 1 ecolsys-112414-054424
- 2 29. Watters, J. V., Lema, S. C. & Nevitt, G. A. Phenotype management: a new
3 approach to habitat restoration. *Biol. Conserv.* **112**, 435–445 (2003).
- 4 30. Quinn, T. P., Hodgson, S., Flynn, L., Hilborn, R. & Rogers, D. E. Directional
5 selection by fisheries and the timing of sockeye salmon (*Oncorhynchus nerka*)
6 migrations. *Ecol. Appl.* **17**, 731–739 (2007).
- 7 31. Laugen, A. T. *et al.* Evolutionary impact assessment: accounting for
8 evolutionary consequences of fishing in an ecosystem approach to fisheries
9 management. *Fish Fish.* **15**, 65–96 (2014).
- 10 32. Heino, M. *et al.* Can fisheries-induced evolution shift reference points for
11 fisheries management? *Ices J. Mar. Sci.* **70**, 707–721 (2013).
- 12 33. Jørgensen, C. *et al.* Ecology: managing evolving fish stocks. *Science* **318**, 1247–
13 1248 (2007).
- 14 34. Kuparinen, A. & Hutchings, J. A. Consequences of fisheries-induced evolution
15 for population productivity and recovery potential. *Proc. R. Soc. B* **279**, 2571–
16 2579 (2012).
- 17 35. Garcia, S. M. *et al.* Conservation. Reconsidering the consequences of selective
18 fisheries. *Science* **335**, 1045–1047 (2012).
- 19 36. Carlson, S. M. & Seamons, T. R. A review of quantitative genetic components of
20 fitness in salmonids: implications for adaptation to future change. *Evol. Appl.*
21 **1**, 222–238 (2008).
- 22 37. Knapp, R. A., Boiano, D. M. & Vredenburg, V. T. Removal of nonnative fish
23 results in population expansion of a declining amphibian (mountain yellow-

- 1 legged frog, *Rana muscosa*). *Biol. Conserv.* **135**, 11–20 (2007).
- 2 38. Pister, E. P. Wilderness fish stocking: history and perspective. *Ecosystems* **4**,
- 3 279–286 (2001).
- 4 39. Vredenburg, V. T. *et al.* Concordant molecular and phenotypic data delineate
- 5 new taxonomy and conservation priorities for the endangered mountain
- 6 yellow-legged frog. *Journal of Zoology* **271**, 361–374 (2007).
- 7 40. Prchalova, M. *et al.* Size selectivity of standardized multimesh gillnets in
- 8 sampling coarse European species. *Fish. Res.* **96**, 51–57 (2009).
- 9 41. Blanchfield, P. J. & Ridgway, M. S. Reproductive timing and use of redd sites by
- 10 lake-spawning brook trout (*Salvelinus fontinalis*). *Can J Fish Aquat Sci* **54**, 747–
- 11 756 (1997).
- 12 42. R Core Team. R: a language and environment for statistical computing. (2013).
- 13 43. Bates, D., Maechler, M., Bolker, B. M. & Walker, S. Fitting Linear Mixed-Effects
- 14 Models Using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
- 15 44. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest: Tests in
- 16 Linear Mixed Effects Models. R package version 2.0-30. (2016).

17

18 **Acknowledgments**

19 We thank the dozens of individuals who have been involved in the removal of

20 invasive trout in the Sierra Nevada as well as the National Park Service (particularly

21 Ninette Daniele, Travis Espinoza, and Daniel Boiano) and California Department of

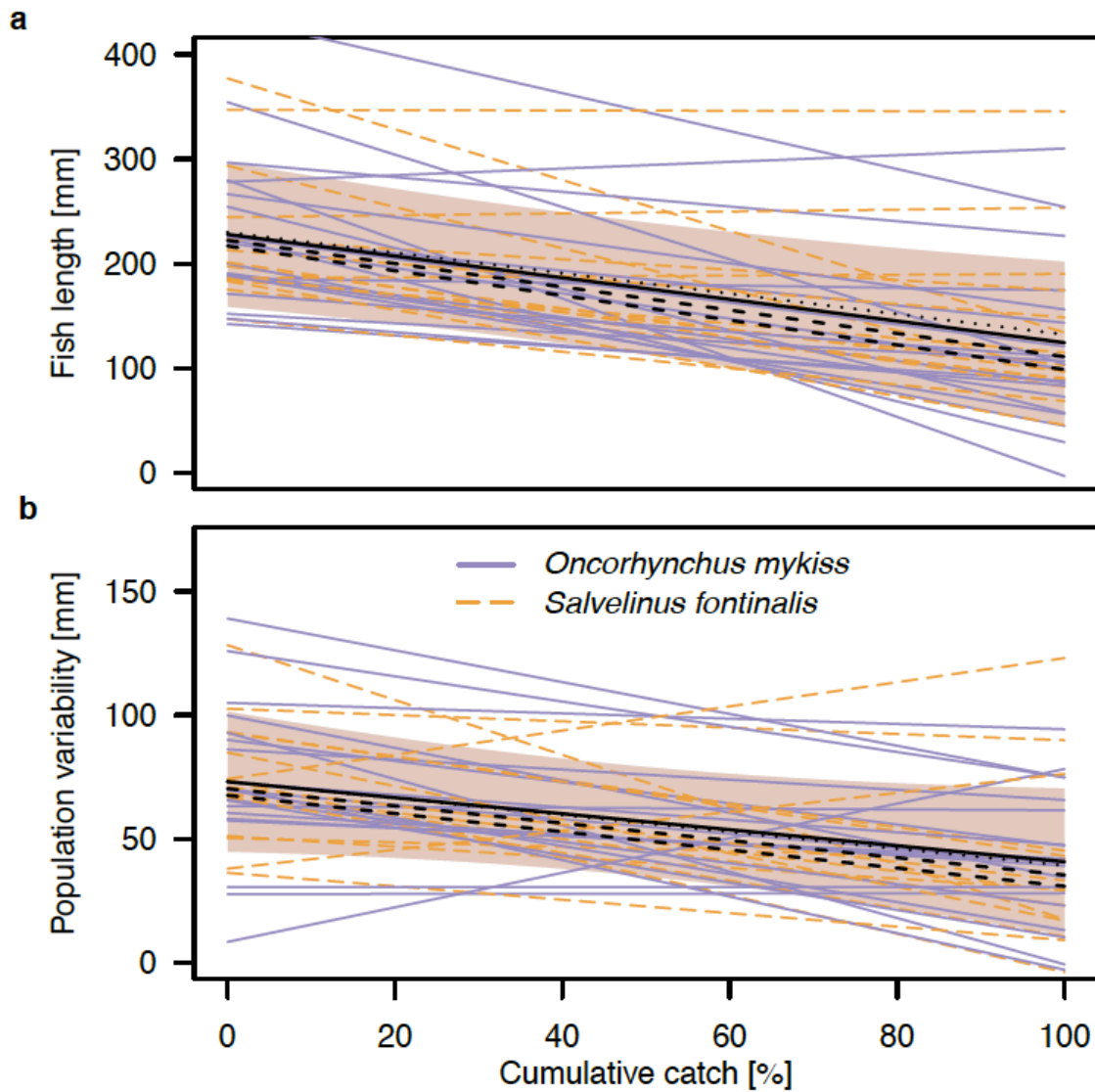
1 Fish and Wildlife (particularly Mitch Lockhart and Sarah Mussulman) for sharing the
2 data collected. SN was funded by the Swiss National Science Foundation
3 (P2LAP3_148434) and the Parrotia Foundation and APH was supported by a
4 Visiting Miller Professorship from the Miller Institute at UC-Berkeley.

5 **Authors contributions**

6 SN and SMC conceived the project. SN analyzed the data. SN, APH, AMS, and SMC
7 discussed the analyses and wrote the manuscript. RAK and MTB collected data and
8 provided feedback on the manuscript.

1 Figures

2 [Figure 1](#)



3

4 **Figure 1: Effect of size-selective fishing on population structure.** Plots
5 demonstrate length-at-capture in mm ($p < 0.001$) (a) and surviving population's
6 length variability (standard deviation) ($p < 0.001$) (b) as a function of the
7 percentage of the population removed to date (i.e., the 'catch intensity'). Thin lines

1 represent the response of individual populations (linear regressions), and bold lines
2 represent the average response of both *Salvelinus fontinalis* (brook trout; dashed
3 orange) and *Oncorhynchus mykiss* (rainbow trout and hybrids; solid purple)
4 populations (mixed-model). Black dashed lines represent the average response
5 using 5% and 10% growth corrections, and black dotted lines represent the
6 response with correction for reproduction after the initiation of the experimental
7 fisheries (see Methods). Shaded area represents mean estimates \pm standard
8 deviation. Analyses were based on 43,827 individuals in 35 populations in (a), and
9 1092 standard deviation estimates in(b) (population details reported in Extended
10 Table 1).

11

1 **Figure 2 – random permutations**

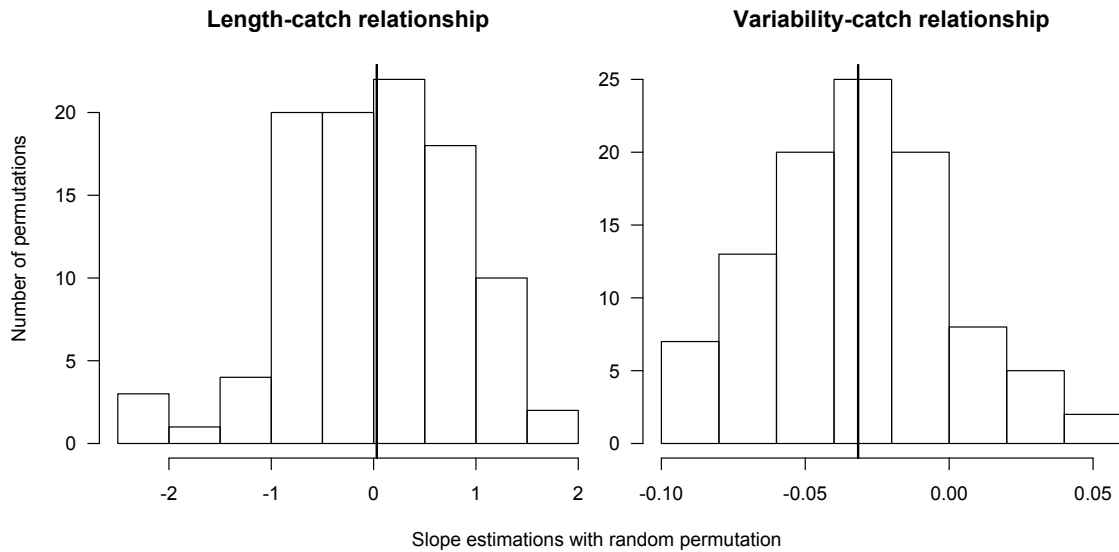
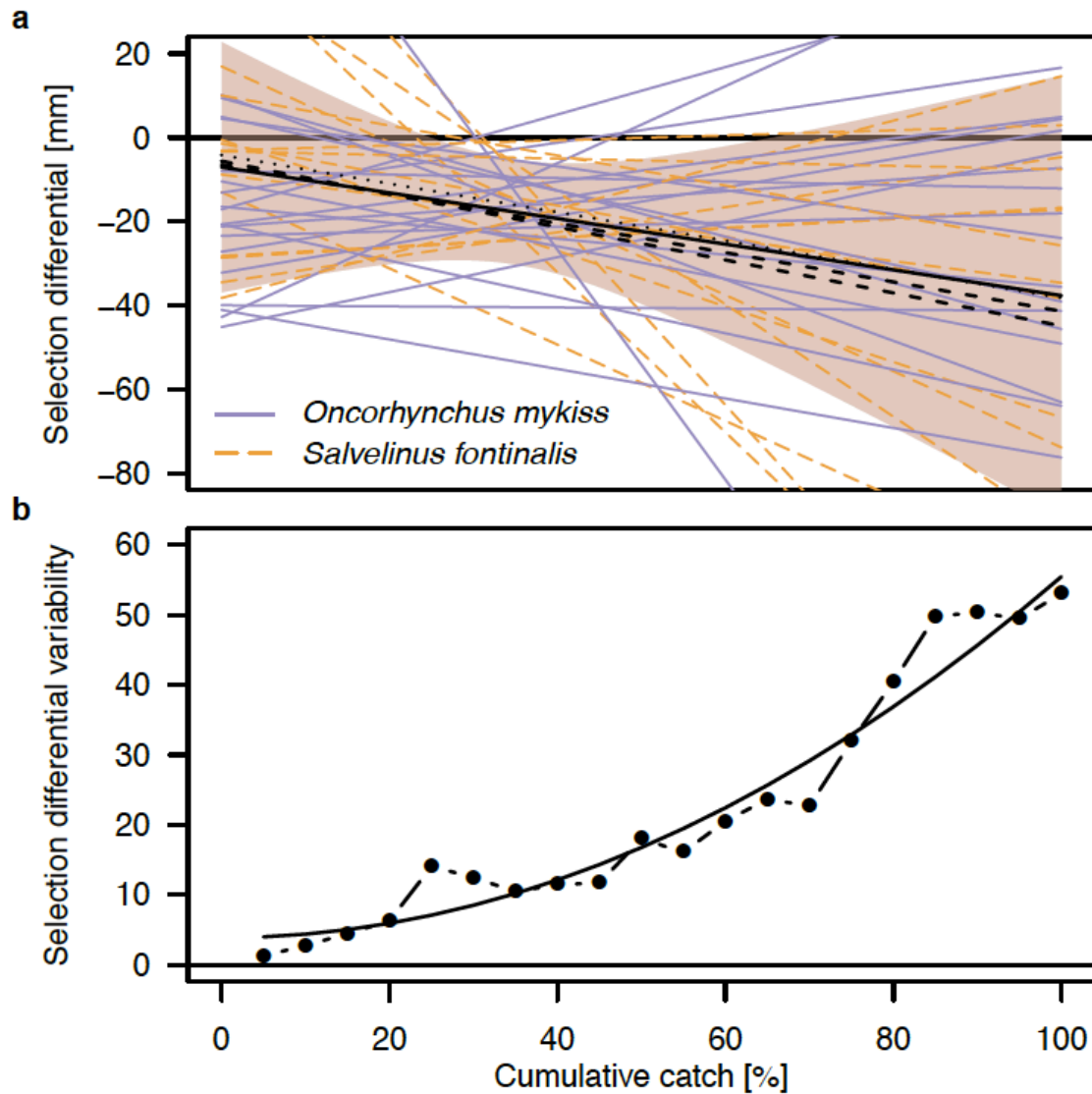


Figure 2: Empirical distributions of the slopes of the length-catch and variability-catch relationships inferred from random permutations of the date at-capture. These distributions represent the expected values of the relationship if fishing is random with respect to size (100 random permutations). Random fishing is not expected to alter the size structure of the population (left-hand panel, slope of the length-catch relationship is 0.08 ± 1.00 , not significantly different from zero). Random fishing is expected to slightly reduce variability (right-hand panel, slope of variability-catch relationship = -0.03 ± 0.04), but less than non-random fishing where the slope of the variability-catch relationship is expected to be ten times larger ($0.32 \text{ mm} \pm 0.07 \text{ mm}/\%$).

1 **Figure 3**



2

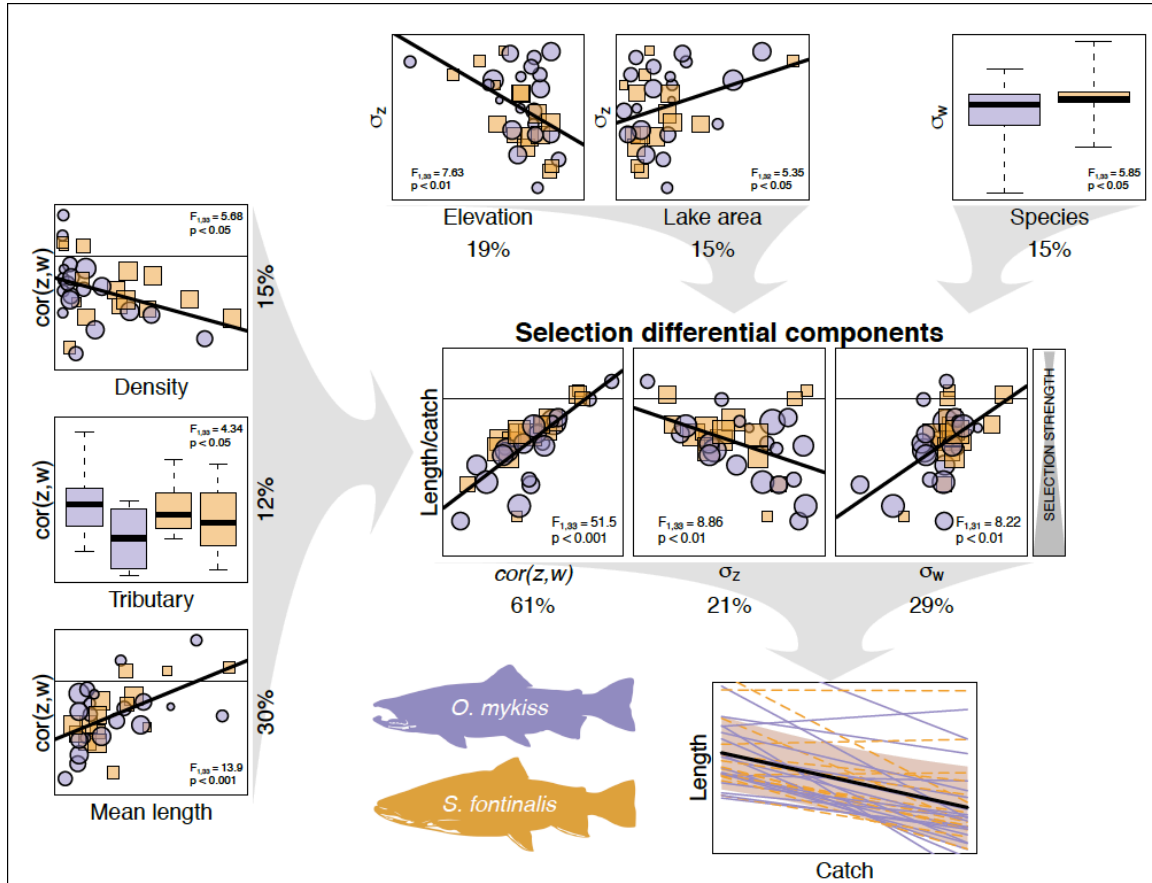
3 **Figure 3: Effect of cumulative catch on the selection differential. Plots**

4 demonstrate the selection differential, that is, the difference in mean length between
5 the initial population (i.e., before fishing) and the survivors (i.e., after fishing) (linear
6 mixed model, $p < 0.05$) (a) and selection differential variability (standard deviation)
7 (quadratic model, $p < 0.001$) (b) as a function of the percentage of the population

1 removed to date (i.e., catch intensity). Thin lines represent the responses of
2 individual populations, and bold lines represent the average response of both
3 *Oncorhynchus mykiss* (rainbow trout and hybrids; solid purple) and *Salvelinus*
4 *fontinalis* (brook trout; dashed orange) populations. Dashed black lines represent
5 the average response using 5% and 10% growth corrections, and black dotted lines
6 represent the response with correction for reproduction after the initiation of the
7 experimental fisheries (see Methods). We used 1092 selection differentials
8 estimates from 35 populations in (a), and one standard deviation estimate per 5%
9 fraction of catch in (b) (population details reported in Extended Table 1).

1 **Figure 4**

2



3

4 **Figure 4: Schematic to show the main drivers of fishing-induced selection.** The

5 length-catch relationship (bottom-right) represents selection, as expressed in Figure

6 1a. The three central plots represent the selection differential components (fitness-

7 trait correlation, trait variability, fitness variability) and the relationship between

8 each component and the length-catch relationship, orange circle for rainbow trout

9 and purple square for brook trout (symbol size is proportional to log-transformed

10 population size). The regression statistics are included on each plot. The percentage

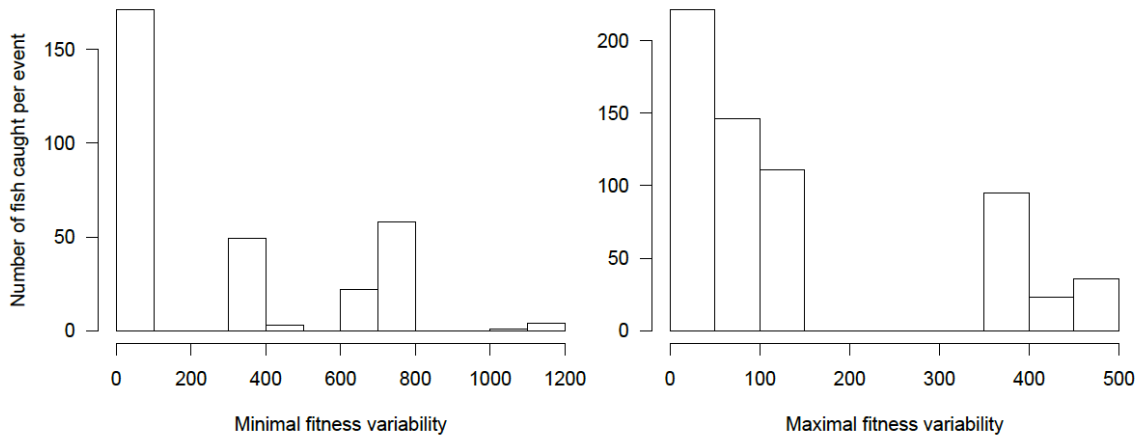
11 displayed below each plot represents the univariate proportion of variance

1 explained (note that these do not add up to 100%, as they can be correlated). Using
2 a multivariate model, the proportion of variance would be: 44% for the correlation,
3 21% for trait variability, and 17% for fitness variability. The six remaining plots (on
4 the left and top) represent the influence of environmental, demographic, and
5 species-specific factors on the selection components. The proportion of variance in a
6 multivariate model explaining the correlation between trait and fitness (left-hand
7 plots) is 29.6% for mean length, 13.8% for the presence of a tributary, and 4.2% for
8 density, and the proportion of variance in a multivariate model explaining the length
9 variability (top-left) is 18.8% for elevation, and 8.6% for lake area.

10

1 Extended Figure 1 – Catch distribution

2



3

Catch distribution over the study duration

4 **Extended Figure 1: representations of the two most extreme catch**
5 **distributions determining the fitness variability. For the population on the**
6 **left-hand panel, the fitness variability was minimal and fishing was relatively**
7 **evenly distributed throughout the study period. For the population on the**
8 **right-hand panel, the fitness variability was maximal, and fishing events were**
9 **distributed at the start and end of the study.**

10

1 Ext. Table: Environmental and population specific parameters

Species	Perimeter [m]	Area [m ²]	Elevation [m]	Max depth [m]	Tributary	Pop. size [ind]	Pop. density [ind/ha]	Study duration [days]	Number of fishing events	Prop. of fish caught by gillnets	Average length [mm]	Length stand. dev. [mm]	Length max [mm]
Rainbow	2118	47270	2146	18	FALSE	120	25.4	717	17	1.00	336	88	530
Brook	969	17129	2566	4.1	TRUE	257	150.0	275	7	1.00	168	82	344
Rainbow	1030	23610	3318	10	FALSE	375	158.8	653	18	0.70	127	86	352
Brook	981	33508	3380	12.6	FALSE	4397	1312.2	701	114	0.90	199	63	335
Rainbow	981	33508	3380	12.6	FALSE	93	27.8	392	24	1.00	296	27	379
Brook	470	14116	3408	5.3	FALSE	4736	3355.1	689	105	0.85	142	53	265
Brook	531	15017	3492	3.2	FALSE	632	420.9	486	33	1.00	188	35	309
Rainbow	1167	36730	3010	14.1	TRUE	19	5.2	383	5	1.00	256	70	390
Brook	456	8855	3157	8.5	FALSE	1004	1133.8	3307	32	1.00	143	52	275
Brook	457	11122	3266	2.7	FALSE	2804	2521.1	1476	51	0.85	130	46	310
Brook	740	25365	3300	8.7	FALSE	4542	1790.7	1814	57	0.97	148	52	284
Rainbow	1384	81257	2949	13.8	FALSE	3821	470.2	1841	61	0.55	115	79	460
Rainbow	1162	70134	3338	30	FALSE	81	11.5	29	9	1.00	179	58	250
Rainbow	757	14758	3133	4	FALSE	1976	1338.9	1834	67	0.91	149	58	275
Rainbow	1552	102109	3510	22.5	FALSE	1642	160.8	1131	31	1.00	210	93	450
Rainbow	283	5008	3510	7	FALSE	884	1765.2	792	22	1.00	115	53	250
Rainbow	853	34055	3358	4.5	TRUE	599	175.9	1431	24	1.00	173	53	328
Brook	562	20472	3047	4.6	TRUE	69	33.7	36	5	1.00	251	94	380
Rainbow	833	30659	3583	7.8	FALSE	345	112.5	747	13	1.00	184	41	312
Brook	871	35722	3218	8.5	FALSE	3803	1064.6	751	59	0.75	144	73	250
Rainbow	871	35722	3218	8.5	FALSE	60	16.8	447	21	0.50	124	81	250
Rainbow	805	44565	3115	16	FALSE	807	181.1	437	43	1.00	214	92	420
Brook	482	12109	3516	5	FALSE	485	400.5	397	28	1.00	188	38	257
Brook	759	37403	3509	25	FALSE	4741	1267.5	1158	41	1.00	105	59	350
Brook	207	1989	2972	5	TRUE	56	281.5	38	5	1.00	220	77	359
Brook	1330	57880	2987	15	FALSE	2764	477.5	698	19	1.00	127	58	302
Brook	527	11553	3214	4	FALSE	1946	1684.4	487	73	0.56	112	73	250
Rainbow	527	11553	3214	4	FALSE	45	39.0	473	21	0.80	138	66	200
Rainbow	578	18206	3188	10	FALSE	1437	789.3	1455	45	1.00	114	43	320
Rainbow	854	37123	2903	10	FALSE	98	26.4	1833	18	0.28	131	77	370
Rainbow	252	2267	3344	2.5	TRUE	639	2818.7	421	20	0.60	113	64	278
Rainbow	418	10980	3347	5.5	TRUE	302	275.0	420	14	0.32	93	90	315
Rainbow	688	23470	3408	11	FALSE	1539	655.7	450	29	0.48	115	75	360
Rainbow	356	7220	3402	7	FALSE	308	426.6	1161	25	1.00	132	82	348
Brook ₂	1444	124625	2815	10	FALSE	253	20.3	68	23	1.00	347	89	550