Transactions of the American Fisheries Society 148:552–568, 2019
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ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10160

FEATURED PAPER

Experimental Size-Selective Harvesting Affects Behavioral Types of a Social Fish

Valerio Sbragaglia
Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany; and Institute for Environmental Protection and Research, Via del Cedro 38, Livorno 57122, Italy

Josep Alós
Instituto Mediterráneo de Estudios Avanzados (Consejo Superior de Investigaciones Científicas, Universitat de les Illes Balears), C/Miquel Marqués 21, Esporles, Illes Balears 07190, Spain

Kim Fromm and Christopher T. Monk
Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

Carlos Díaz-Gil
Instituto Mediterráneo de Estudios Avanzados (Consejo Superior de Investigaciones Científicas, Universitat de les Illes Balears), C/Miquel Marqués 21, Esporles, Illes Balears 07190, Spain

Silva Uusi-Heikkilä
Section of Natural Resources and Environment, Department of Biological and Environmental Science, University of Jyväskylä, Post Office Box 35, Jyväskylä 40014, Finland

Andrew E. Honsey
Ecology, Evolution, and Behavior Graduate Program, University of Minnesota, St. Paul, Minnesota 55108, USA

Alexander D. M. Wilson
School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

Robert Arlinghaus*
Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany; and Division of Integrative Fisheries Management, Department of Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Berlin, Germany

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Abstract

In most fisheries, larger fish experience substantially higher mortality than smaller fish. Body length, life history, and behavioral traits are often correlated, such that fisheries-induced changes in size or life history can also alter

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*Corresponding author: arlinghaus@igb-berlin.de
Received July 30, 2018; accepted March 5, 2019

behavioral traits. However, empirical evidence regarding how size-selective harvesting alters the evolution of behavioral traits in exploited stocks is scarce. We used experimental lines of Zebrafish *Danio rerio* that were exposed to positively size-selective, negatively size-selective, or random harvest over five generations. Our aim was to investigate whether simulated fishing changed the mean personality of the surviving females five generations after initial harvesting halted. We found that mean boldness, activity, and sociability were significantly altered relative to the randomly harvested control line. Harvest-induced changes in individual-level personality were only detected in the negatively size-selected line. By contrast, we did not detect harvest-induced evolution of personality in the positively size-selected line. We conclude that size-selective harvesting alters individual personality in this social fish.

In most exploited fish stocks, fishing mortality on adults is substantially greater than natural mortality (Brown et al. 2008). In addition, most fishing gears and harvest regulations operate in a size-selective manner (Jørgensen et al. 2007; Kuparinen et al. 2009; Pierce 2010). Such selection can lead to life history adaptations within just a few generations (Jørgensen et al. 2007; van Wijk et al. 2013; Laugen et al. 2014; Heino et al. 2015; Uusi-Heikkilä et al. 2015). Fast life history traits—characterized by fast juvenile growth, early maturation at small size, and elevated reproductive investment (Stearns 1992)—are generally (but not necessarily; Dunlop et al. 2015; Gíslason et al. 2018) favored under intensive harvesting in both unselective and positively size-selective scenarios (i.e., preferential harvest of large individuals), leading to reduced postmaturation growth and terminal length (Jørgensen et al. 2007) and yielding elevated natural mortality (Jørgensen and Holt 2013; Andersen et al. 2018). Most research on fisheries-induced evolution (FIE) has focused on life history adaptation (Sharpe and Hendry 2009; Devine et al. 2012), with much less attention devoted to the evolution of behavioral and physiological traits (Heino and Godø 2002; Uusi-Heikkilä et al. 2008; Philipp et al. 2009; Heino et al. 2015; Arlinghaus et al. 2017; Hollins et al. 2018).

In this context, fish personality traits (individual behavioral differences that are consistent over time and/or across situations; Reale et al. 2007) are candidates for the FIE of behavior through two main pathways (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Arlinghaus et al. 2017). First, traits such as boldness are related to fitness (e.g., Smith and Blumstein 2008) and are often correlated with life history traits (growth rate, reproductive investment, maturation size, and longevity; Réale et al. 2010; Dammhahn et al. 2018); thus, behavioral traits can evolve whenever the fitness landscape changes (Jørgensen and Holt 2013; Andersen et al. 2018; Claireaux et al. 2018). For example, life history adaptations to fishing pressure selecting for a fast life history favor individuals that forage intensively and/or aggressively to reap fitness benefits early in life (Jørgensen and Holt 2013; Andersen et al. 2018; Claireaux et al. 2018). Second, heritable traits, including boldness or aggression (Dochtermann et al. 2015), are often systematically related to vulnerability to fishing; thus, personality traits can be under direct selection by fisheries (Rudstam et al. 1984; Wilson et al. 2011, 2015; Sutter et al. 2012; Härkönen et al. 2014; Diaz Pauli et al. 2015; Alós et al. 2016; Arlinghaus et al. 2017; Diaz Pauli and Sih 2017; Klefoth et al. 2017). Importantly, the heritability of personality traits is comparable to or even higher than the heritability of life history and morphological traits (Mousseau and Roff 1987; Stirling et al. 2002; Dochtermann et al. 2015). Therefore, direct selection on personality can lead to adaptive evolution of behavior to fishing without corresponding changes in life histories (Biro and Post 2008; Sutter et al. 2012; Biro and Sampson 2015; Alós et al. 2016; Arlinghaus et al. 2017; Monk and Arlinghaus 2017). Finally, behavior can also plastically change in exploited fish stocks due to learning or due to relaxation of density dependence (e.g., Raat 1985; Özbilgin and Glass 2004; Januchowski-Hartley et al. 2011; Klefoth et al. 2013; Sbragaglia et al. 2018).

Irrespective of the exact mechanism (genetic or plastic), it is important to consider both evolutionary and ecological aspects of fisheries-induced effects on stock dynamics (Eikeset et al. 2016). Fish personality can have profound consequences for social functioning, population dynamics, ecosystem processes, and fisheries (Conrad et al. 2011; Palkovacs et al. 2012, 2018; Wolf and Weissing 2012; Mittelbach et al. 2014; Ward et al. 2016; Arlinghaus et al. 2017; Diaz Pauli and Sih 2017). However, the findings of empirical studies investigating the relationship between behavior and vulnerability to fishing are inconsistent; therefore, a conclusive understanding of the FIE of personality traits is currently lacking (e.g., Wilson et al. 2011, 2015; Sutter et al. 2012; Härkönen et al. 2014; Kekäläinen et al. 2014; Biro and Sampson 2015; Diaz Pauli et al. 2015; Alós et al. 2016; Vainikka et al. 2016; Monk and Arlinghaus 2017; Thambithurai et al. 2018). Moreover, there are only a few theoretical studies focused on the effects of selective harvesting on the evolution of fish personality, and these studies have largely focused on boldness as the focal trait under selection (Andersen et al. 2018; Claireaux et al. 2018). Hence, there is limited knowledge of the evolutionary effects of fishing on personality traits.

Selection experiments in the laboratory can provide cause-and-effect evidence regarding the FIE of both life history and personality traits (Diaz Pauli and Heino 2014). The few existing experimental harvesting studies focused on personality and behavioral traits suggest that negative size-selective harvesting increases the propensity to take risks (Walsh et al. 2006; Uusi-Heikkilä et al. 2015), in agreement with theoretical models (Andersen et al. 2018; Claireaux et al. 2018). We built on the results presented by Uusi-Heikkilä et al. (2015) to investigate the evolutionary change in a range of personality traits in response to both positive and negative size-selective harvesting by using the Zebrafish *Danio rerio* as a model organism. Earlier work using Zebrafish selection lines that were created by imposing a 75% per generation mortality rate based on size revealed substantial changes in life histories, size variation, allele frequencies, and transcriptome profiles but no change in metabolic rates after just five generations of harvesting (Uusi-Heikkilä et al. 2015, 2016, 2017). Negative size selection triggered evolutionary adaptations typical of a slow life history (in particular, a lower degree of reproductive investment compared to the control), while positive size selection triggered adaptations characteristic of a fast life history (young age and small size at maturation, high relative fecundity, and small terminal length). Most importantly, Uusi-Heikkilä et al. (2015) documented that negative size selection led to evolutionary changes in behavior by increasing boldness at the juvenile stage. However, sexual maturation is a critical transition during life history (Bernardo 1993) and is known to alter animal personality traits, such as boldness and aggression (e.g., DiRienzo et al. 2012; Gyuris et al. 2012; Niemelä et al. 2012), both of which are important for reproduction (McPeek 2004; Niemelä et al. 2012). It is thus unclear whether the evolutionary changes in boldness reported for the juvenile stage by Uusi-Heikkilä et al. (2015) hold for the adult life stage and whether personality traits other than boldness (i.e., sociability, aggression, and activity) also change in response to size-selective harvesting.

Our objective was to examine the effects of five generations of intensive directional size selection (both positive and negative) on four different adult personality traits (activity, boldness, aggression, and sociability) measured at the individual level (i.e., not in a group context). Because sex-specific behavioral differences have been described in Zebrafish (Spence et al. 2008) and pace-of-life syndromes can be sex-specific (Hämäläinen et al. 2018), we tested our hypotheses only with females. Following the theoretical model of Andersen et al. (2018), we predicted that positive size selection (mimicking a fishery with a minimum length limit) favored the evolution of shy adult individuals. By contrast, we expected the evolution of bold adult individuals in the negative size-selection line (mimicking a fishery with a maximum size limit). We also formulated predictions regarding evolutionary change in three additional personality traits (activity, aggression, and sociability), assuming that these traits are linked to boldness by a behavioral syndrome (Sih et al. 2004; Réale et al. 2010; Conrad et al. 2011). Specifically, we predicted that Zebrafish exposed to positive size selection (where small fish had a selective advantage) would be (1) less active, (2) less aggressive, and (3) more social than fish of the control line. We expected opposing adaptations in relation to negative size selection (where large fish had a selective advantage). We also predicted that all four behavioral traits would be repeatable over time (i.e., indicative of personality traits; Reale et al. 2007) and correlated amongst one another (i.e., indicative of a behavioral syndrome; Sih et al. 2004), as already demonstrated in previous studies on Zebrafish (e.g., Moretz et al. 2007; Dahlbom et al. 2011; Ariyomo et al. 2013; Toms and Echevarria 2014). Given that personality is correlated with body size in Zebrafish (Polverino et al. 2016a) and knowing that the Zebrafish selection lines we studied differ in adult body size (Uusi-Heikkilä et al. 2015; see also Figure 1), it is possible that size differences among the selection lines could mask evolutionary adaptation in personality. We thus included and excluded body size (TL) as a covariate in our analysis to reveal whether selection treatment per se affected the evolution of personality or whether changes in the size of fish indirectly altered behaviors in the evolved lines.

METHODS

Selection Lines

Four experimental Zebrafish lines (two lines per treatment) were exposed to directional selection pressures (a 75% per generation harvest rate) acting on either large body size (large-harvested line; $N = 2$) or small body size (small-harvested line; $N = 2$). Two additional replicated control lines were harvested randomly with respect to size (random-harvested line; $N = 2$; Uusi-Heikkilä et al. 2015). Size-selective harvesting occurred during the first five generations (F_1 to F_5) once 50% of the randomly harvested control fish were mature. Harvesting was stopped for the succeeding generations to remove any "maternal" effects and allow the singling out of the evolutionary outcomes of selection as well as the maintenance of evolutionary adaptations (Uusi-Heikkilä et al. 2015). Zebrafish lines were reared in groups within six separate tanks in a common recirculation system under the following conditions: water temperature was maintained at 26 ± 0.5°C, photoperiod was set to a 12-h light : 12-h dark cycle (light on at 0700 hours), and the fish were fed ad libitum with dry food (TetraMin; Tetra) five times per day during daylight.

Given the common-garden design and a single factor being different among the selection lines (i.e., harvesting), comparisons among lines starting from F_8 (i.e., three generations after initial harvesting halted) onward are

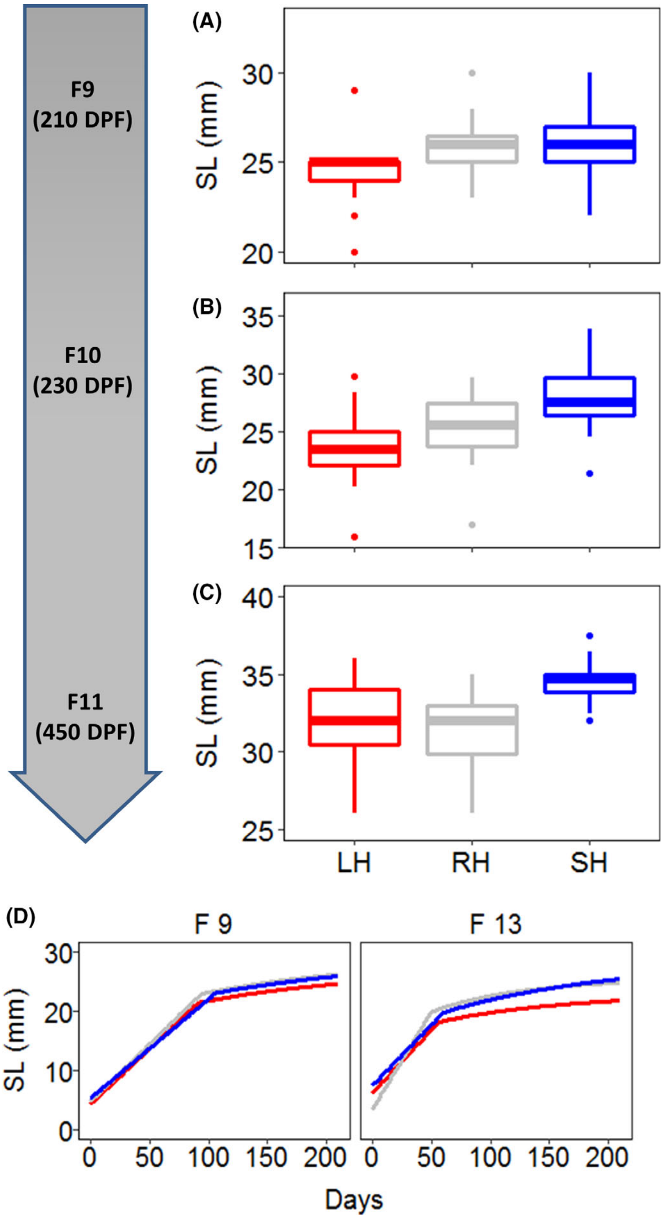

FIGURE 1. Differences in size (mm SL) among positive (large-harvested line [LH]) and negative (small-harvested line [SH]) size-selected Zebrafish lines with respect to the control line (RH) that was randomly selected for size are presented across ontogeny: **(A)** F_9 (LH: $N = 19$; RH: $N = 15$; SH: $N = 21$) at 210 d postfertilization (DPF), **(B)** F_{10} ($N = 100$) at 230 DPF, and **(C)** F_{11} ($N = 30$) at 450 DPF. **(D)** Results of the Lester biphasic growth model are also presented for the F_9 and F_{13} generations. More details regarding the statistical approach are presented in the Supplementary Material available in the online version of this article.

indicative of evolutionary adaptations to size-selective harvesting, and earlier analyses revealed that genetic changes have indeed taken place (Uusi-Heikkilä et al. 2015). The first life history and lifetime growth outcomes were assessed at F_9, revealing that the large-harvested line evolved a smaller adult length due to altered energy allocation patterns and increased relative fecundity (Uusi-Heikkilä et al. 2015; Figure 1), while the small-harvested line evolved a lower reproductive investment (Uusi-Heikkilä et al. 2015). Despite the potential for evolutionary rebound (Conover et al. 2009; Salinas et al. 2012), the evolved differences in life histories and terminal length in the Zebrafish lines were still maintained at F_{13} (see Supplementary Material and Figure 1), demonstrating that recovery has not taken place for the life history traits affecting lifetime growth.

Experimental Procedure

We used individuals from the F_{10} generation of the selection lines (Uusi-Heikkilä et al. 2015, 2017). One month before the beginning of the behavioral experiment, about 50 fish from each of the six selection line replicates were randomly selected from the common recirculation system, moved to six acclimation aquaria (30 × 40 × 30 cm), and fed twice per day (dry food at 2% of fish biomass). At the beginning of the behavioral experiments, 15 females from each of the six selection lines were randomly selected from the acclimation aquaria, measured for TL, and kept in social isolation tanks (30 × 12 × 12 cm) for 24–36 h before the experimental trials started.

We used three individual-level experimental trials to study four different individual behaviors in the following order: total activity (swimming activity in the test tank) and boldness (i.e., activity in a risk zone, measured in the same test environment as total activity), aggression, and sociability. We determined the repeatability score of each behavior (an indicator of consistent between-individual differences in behaviors; Bell et al. 2009) by repeating the assays after 24 h in the same order. All trials ran between 1300 and 1800 hours. The fish were transferred from the individual isolation tank to the experimental arena with a dip net. A web camera (Logitech C920 HD Pro; http://www.logitech.com) was placed above the experimental arena, and a 5-min video was recorded for each individual trial. The video recording started 60 s after the fish was placed into the experimental arena to allow for a brief acclimation period.

Activity and boldness trial.— Total activity and boldness were tested during the same experimental trial in a standard open-field arena (30 × 30 cm; 4-cm water level) in which all of the walls were covered with black foil to avoid reflections. An open-field test is a common approach for studying Zebrafish behavior and can also be associated with exploration of a novel environment (Stewart et al. 2012; Polverino et al. 2016a). In our study, activity was defined as the total distance traveled by fish in the entire area of the arena, whereas risky activity was defined as the total distance traveled by fish in the central area of the arena: a square area with edges at a distance of two body lengths from all four walls for each fish. The central part of the arena is usually associated with risk by Zebrafish (Kalueff et al. 2013). The total distance covered in the arena was estimated using automated tracking of Zebrafish with EthoVision XT 9 (Noldus). EthoVision tracks were subsequently analyzed using a customized R script (R version 3.2.2) to automatically correct for the size of the fish and account for any shifts in camera perspective.

Aggression trial.— Aggressive behavior was assessed by using a mirror test, which is a common test for studying Zebrafish agonistic behavior (e.g., Gerlai et al. 2000; Pham et al. 2012). Trials were run in an experimental arena (30 × 30 cm; 4-cm water level) in which all of the walls were covered with black foil except for one, over which a mirror was placed. Levels of aggression were estimated as the number of charges the fish displayed toward its image on the mirror (Larson et al. 2006). A charge was scored when the fish suddenly accelerated toward the mirror from a distance of at least two body lengths, as defined in previous Zebrafish studies (Gerlai et al. 2000; Ariyomo and Watt 2012).

Sociability trial.— Social behavior was tested in an experimental arena (68 × 30 cm; 4-cm water level) that was subdivided into two areas by means of a transparent plastic divider. One area (38 × 30 cm) was occupied by the focal fish, while the other area (30 × 30 cm) was occupied by a stimulus shoal—a group of 13 randomly selected female Zebrafish (replaced every day). All arena walls except the wall occupied by the plastic divider were covered with black plastic. Sociability in Zebrafish has been previously assessed using similar methods (Pham et al. 2012; Nunes et al. 2017). Sociability was estimated as the number of attempts the focal fish made to join the stimulus shoal. An attempt was scored when the fish suddenly accelerated toward the divider from a distance of at least two body lengths.

Statistical analysis.— We used generalized linear mixed-effects models (GLMMs) to (1) test for differences among selection lines (large-harvested, small-harvested, and random-harvested) in the four behaviors (total activity, risky activity, aggression, and sociability); and (2) decompose the variance into between- and within-individual sources and estimate the repeatability scores (*R*) of these four traits while controlling for significant differences in selection lines (adjusted-*R*). For each of the four behaviors, we fitted two different GLMMs using the R library "MCMCglmm" (Hadfield 2010; Dingemanse and Dochtermann 2013; Harrison et al. 2014; Alós et al. 2017). The first GLMM included selection line (a factor with three levels) as a fixed effect and included the identity of the fish and the replicate of the selection line as random intercept terms. In this model, we used the entire data set without considering differences in size of the fish among lines (model 1; the global treatment model). The second GLMM (model 2; the size-matched model) included selection line (a factor with three levels) and TL of the fish as fixed effects, and the identity of the fish and the replicate of the selection line were incorporated as random intercept terms. Because selection lines and fish sizes were correlated (Figure S1 available in the Supplement), we selected a subsample of individuals to create a new, size-matched data set in which there were no differences in the mean size and size range among the three selection lines (Figure S1). The parameters, 97.5% credibility intervals, and *P*-values were estimated using a Bayesian Markov chain–Monte Carlo (MCMC; Hadfield 2010) approach and uninformative priors. We drew 30,000 posterior samples and discarded the initial 20,000 iterations (burn-in period); 1 out of 10 of the remaining iterations were kept to prevent autocorrelation (thinning strategy). The convergence of the MCMC chains was assessed by visual inspection of the chains and was tested using the Gelman–Rubin statistic (Plummer et al. 2006). A threshold value of 1.1 or less for the Gelman–Rubin statistic was assumed to indicate convergence (Gelman and Rubin 1992; Hadfield 2010).

Adjusted-*R* was estimated as the quotient of the between-individual variance (the variance across random intercepts attributed to the individuals [V_{ind_0}]) and the sum of V_{ind_0} and the within-individual or residual variance (the variance associated with replicate, measurement error, and phenotypic flexibility [V_{e_0}]) for a given behavioral trait in accordance with previous studies (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013). We extracted V_{ind_0} and V_{e_0} from the four fitted GLMMs and computed the adjusted-*R* values and associated 95% confidence intervals using the posterior probability distributions. To assess the significance of the adjusted-*R* scores, a reduction in the deviance information criterion (DIC; ΔDIC) provided by the GLMM, where V_{ind_0} was constrained to zero, was used to detect significant V_{ind_0}; any ΔDIC larger than 2 was considered to be significant. Total activity, log-transformed risky activity, and sociability models were initially fitted assuming a Gaussian distribution of errors. By contrast, a Poisson distribution of errors was used for aggression data in both models (overdispersion of both models was close to 1.0 in both cases; see Results). For model 1 (the global treatment model), we restricted the analysis to individuals with two observations (trials), resulting in a sample size of 22 individuals for the large-harvested line, 18 individuals for the random-harvested line, and 22 individuals for the small-harvested line (size range = 20–34 mm; see Figure S1). For model 2 (the size-matched model), we further restricted the individuals to those with overlapping size, resulting in a smaller sample size of 15 individuals for the large-harvested line, 18 individuals for the random-harvested line, and 11 individuals for the small-harvested line (size range = 22–28 cm; see Figure S1). Finally, we tested for correlations among repeatable behaviors using Kendall's coefficient (r_τ) to examine evidence of behavioral syndromes (i.e., correlations among the personality traits).

RESULTS

During the 5-min experimental trials, total activity ranged from 1 to 29 m, while activity in the risk zone (i.e., boldness) ranged from 0 to 11 m. Aggressive behavior ranged from 0 to 84 charges. Finally, sociability ranged from 0 to 81 attempts to join the shoal. With the exception of aggression, all behavioral traits tested with model 1 (the global treatment model without controlling for length; Figure 2) were found to be repeatable (total activity: mean adjusted-$R = 0.43$; boldness: mean adjusted-$R = 0.17$; sociability: mean adjusted-$R = 0.37$; Tables 1, 2), and all repeatable traits were interpreted as personality traits. Similar results were obtained with model 2 (the size-matched model; Figure 3), as all traits except for aggression were repeatable (total activity: mean adjusted-$R = 0.42$; boldness: mean adjusted-$R = 0.32$; sociability: mean adjusted-$R = 0.46$; Tables 1, 2). Thus, the aggression test we used did not result in a stable personality trait.

In both models 1 and 2, the small-harvested line was found to be significantly less active ($P < 0.01$) and less social ($P < 0.05$) than the control line (Tables 1, 2; Figure 4). The small-harvested line was significantly less bold ($P < 0.01$) than the control in model 1 and was also less bold (marginally significant at $P = 0.06$) than the control according to model 2 (Table 1; Figure 4). In all cases, there was no significant effect of Zebrafish length, as indicated by the results of model 2 (Tables 1, 2). The large-harvested line did not differ with respect to the control line in any of the personality traits we examined (Tables 1, 2). Aggression was not compared among lines because it was not found to be repeatable (Table 2).

Correlation analysis among the three personality traits indicated that total activity and risky activity were the traits with the strongest positive correlation ($r_\tau = 0.49$–0.52; Table 3). Total activity also exhibited a significant positive correlation with sociability ($r_\tau = 0.34$–0.39; Table 3). Risky activity and sociability demonstrated weak yet significantly positive correlations ($r_\tau = 0.21$–0.26; Table 3), overall revealing evidence for behavioral syndromes.

DISCUSSION

We found that negative size-selective harvesting (the small-harvested line) led to altered mean personality traits in individual female Zebrafish when tested five generations after harvesting halted. By contrast, and contrary to our predictions, positive size-selective harvesting (the large-harvested line) did not alter any of the personality traits that we measured in individual-assayed Zebrafish. Our data indicate that activity, boldness, and sociability decreased in the small-harvested line, while the large-harvested fish did not show differences with respect to the controls. We also found that the differences observed in the personality traits of the small-harvested line did not depend on size and hence constituted an evolutionary adaptation to negative size selection at the behavioral level that was not affected by differences in the average adult sizes among the selection lines. Our findings for adult Zebrafish females generally agreed with an earlier study on juvenile Zebrafish, in which there was no significant difference in average boldness between the large-harvested and control lines (Uusi-Heikkilä et al. 2015). We offer three alternative explanations for our results. The first relates to the pace-of-life syndrome, the second relates to social modulation of individual behavior, and the last relates to predation risk. To underscore our argument, we present additional preliminary results from ongoing experiments in a social context.

Repeatability and Behavioral Syndromes

All behaviors except aggression were found to be repeatable in both models. We used experimental tests that have been previously applied to Zebrafish, such as the open-field test (e.g., Ariyomo and Watt 2012; Polverino et al. 2016a) and the social preference test (e.g., Moretz et al. 2007; Pham et al. 2012; Nunes et al. 2017). Total activity and boldness were most strongly correlated, forming a behavioral syndrome; however, the fact that both measurements were taken in the same experimental trial could mean that we measured two facets of behaviors that are both indicative of one trait primarily (i.e., total activity or boldness). Total activity and sociability also formed a syndrome, indicating that more-active/bold Zebrafish are also more social. Our results agree with previously documented behavioral syndromes in fish (Conrad et al. 2011).

Although the mirror test has been used previously to measure the repeatability of aggression in Zebrafish (e.g., Ariyomo and Watt 2012), we did not find significant repeatability for this trait. Therefore, our results cannot be used to draw conclusions on aggression as a stable personality trait. Similar results were obtained by Way et al. (2015), who compared five different behaviors of Zebrafish by using a mirror test and found that charges displayed by Zebrafish resulted in a nonrepeatable behavior. Despite the fact that charges were described as an aggressive display in other Zebrafish studies (Larson et al. 2006), the mirror test that we used may have been insufficient to consistently motivate individuals across trials (Way et al. 2015). Moreover, a recent study of the Mangrove Rivulus *Kryptolebias*

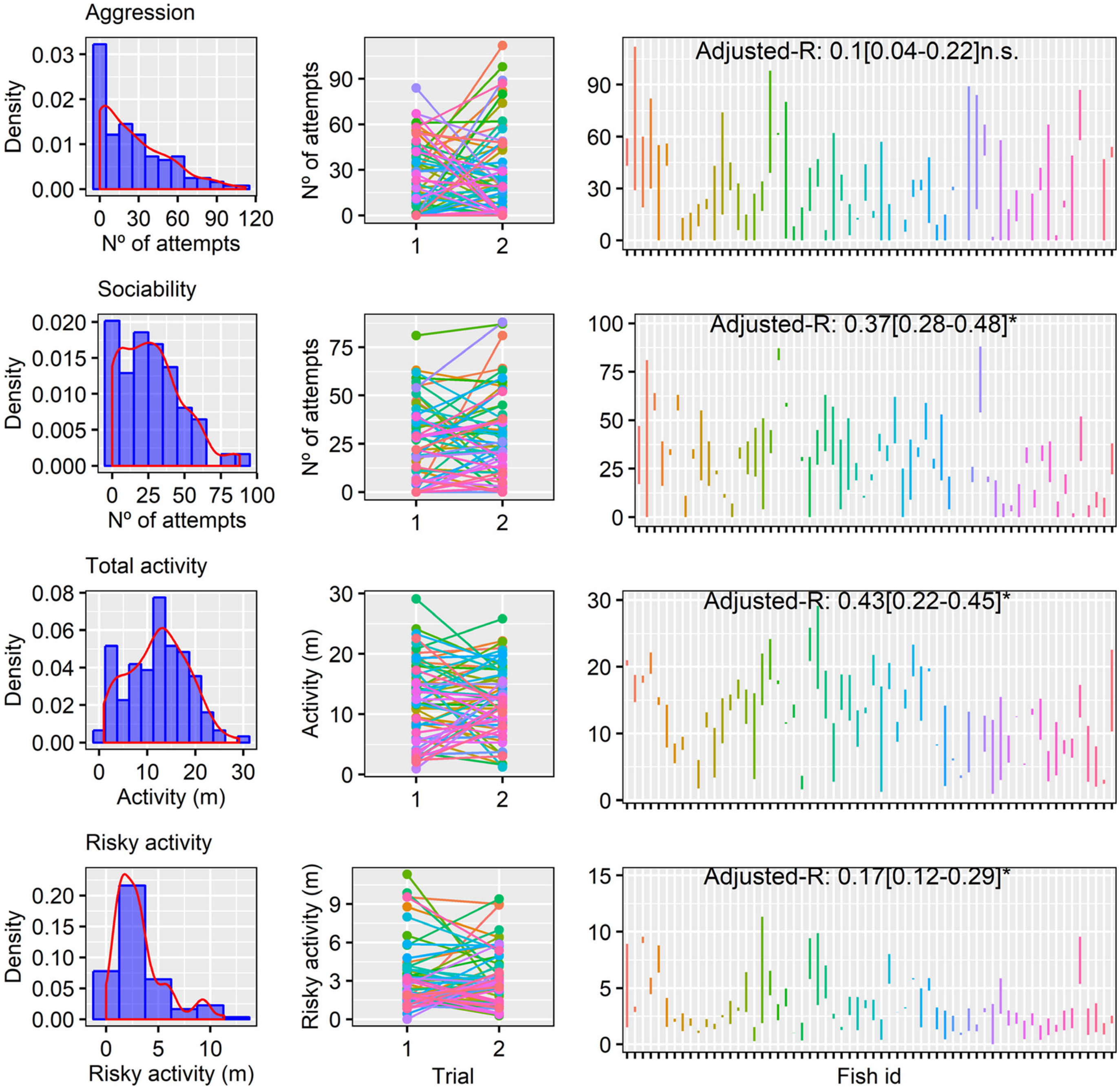

FIGURE 2. Density population plots (left column), trial individual values (middle column), and among-individual differences (right column) for each of the Zebrafish behaviors studied using model 1 (i.e., all individuals were used): aggression, sociability, risky activity, and total activity. The adjusted repeatability score (adjusted-R; with confidence interval in brackets) and significance test results (ns = not significant; $^*P < 0.05$) for each trait are shown.

marmoratus demonstrated that the nonreversing mirror was the only device able to elicit a behavior that predicted fish agonistic behavior during a real fight (Li et al. 2018). For our experiment, we used a normal mirror instead of a nonreversing one, which could have reduced the repeatability of aggression.

Boldness and Activity

Boldness is related to the ability to acquire food resources under risk (Reale et al. 2007). This trait strongly contributes to mediating growth–mortality trade-offs in fishes and other animals (Stamps 2007; Ahrens et al. 2012; Enberg et al. 2012). We documented the existence of

TABLE 1. Estimates of the parameters (posterior mean), lower and upper confidence limits (LCL and UCL), and Markov chain–Monte Carlo (MCMC) *P*-values of the two generalized linear mixed models (model 1 used all individuals; model 2 used individuals with overlapping size and used size as covariate) fitted for total activity and risky activity of Zebrafish. Estimates for positive (large-harvested line [LH]) and negative (small-harvested line [SH]) size-selected lines are shown with respect to the control line that was randomly selected for size (fish TL, cm). The identity of the fish and the selection lines replicate were treated as random intercept terms. Also shown are the deviance information criterion for the constrained model (DIC) and that for the unconstrained model (DIC-un), as well as the adjusted repeatability score (adjusted-*R*), the confidence interval for the adjusted-*R* score (in parentheses), and the significance of the test ($^{\dagger}P < 0.10$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$).

Variable or statistic	Estimate	LCL	UCL	MCMC *P*-value
	Total activity: model 1			
Intercept	14,714	12,348	16,715	<0.001***
Selection line (LH)	−1,080	−3,771	2,172	0.481
Selection line (SH)	−5,984	−8,864	−2,769	<0.001***
DIC = 2,468.9				
DIC-un = 2,498.3				
Adjusted-*R* = 0.43 (0.22–0.45)*				
	Total activity: model 2			
Intercept	24,890	3,050	48,818	0.032*
Selection line (LH)	−1,498	−5,248	2,150	0.414
Selection line (SH)	−5,843	−9,496	−1,903	0.005**
Fish TL (cm)	−4,002	−12,984	4,804	0.383
DIC = 1,759.1				
DIC-un = 1,781				
Adjusted-*R* = 0.42 (0.10–0.45)*				
	Log(risky activity + 1): model 1			
Intercept	8.02	7.60	8.38	<0.001***
Selection line (LH)	−0.11	−0.66	0.34	0.672
Selection line (SH)	−0.68	−1.15	−0.14	0.009**
DIC = 353.7				
DIC-un = 355.8				
Adjusted-*R* = 0.17 (0.12–0.29)*				
	Log(risky activity + 1): model 2			
Intercept	10.39	7.22	13.22	<0.001***
Selection line (LH)	−0.31	−0.74	0.13	0.17
Selection line (SH)	−0.47	−0.98	0.01	$0.06^{\dagger}$
Fish TL (cm)	−0.93	−2.06	0.25	0.12
DIC = 188.7				
DIC-un = 272.1				
Adjusted-*R* = 0.32 (0.1–0.37)*				

behavioral syndromes between boldness and the other repeatable behavioral traits (i.e., activity and sociability); however, our predictions with respect to harvest-induced evolution of average boldness in the large- and small-harvested lines were only partly supported. Although F_{10} juvenile Zebrafish of the small-harvested line were documented to be bolder than controls (Uusi-Heikkilä et al. 2015), we found that contrary to our predictions, F_{10} adult female Zebrafish of the small-harvested line displayed lower levels of average boldness than females in the control line.

Our findings could be related to the pace-of-life syndrome and in particular to a correlation between fast/slow life history and bold/shy personality (Réale et al. 2010; Wright et al. 2018). Previous studies on the same selection lines documented that the small-harvested line maintained fast postmaturation growth at the cost of reduced reproductive investment (Figure 1), indicative of slow life history adaptation (Uusi-Heikkilä et al. 2015). Although the small-harvested line was found to be bolder than the control line at the juvenile stage, we found that adult small-harvested females were shyer than the controls. Thus, the transition at maturation appears to have reversed the personality expressed by the small-harvested line. The pace-of-life hypothesis suggests that fish with slow life histories should be shy to reduce the risk of mortality in favor of future reproduction (Réale et al. 2010; Wright et al. 2018)—a prediction agreeing with our results. Personality changes

TABLE 2. Estimates of the parameters (posterior mean), lower and upper confidence limits (LCL and UCL), and Markov chain–Monte Carlo (MCMC) *P*-values of the two generalized linear mixed models (model 1 used all individuals; model 2 used individuals with overlapping size and used size as covariate) fitted for sociability and aggression of Zebrafish. Estimates for positive (large-harvested line [LH]) and negative (small-harvested line [SH]) size-selected lines are shown with respect to the control line that was randomly selected for size (fish TL, cm). The identity of the fish and the selection lines replicate were treated as random intercept terms. Also shown are the deviance information criterion for the constrained model (DIC) and that for the unconstrained model (DIC-un), as well as the adjusted repeatability score (adjusted-*R*), the confidence interval for the adjusted-*R* score (in parentheses), and the significance of the test (ns = not significant; **P* < 0.05; ****P* < 0.001).

Variable or statistic	Estimate	LCL	UCL	MCMC *P*-value
Sociability: model 1				
Intercept	30.95	23.25	38.85	<0.001***
Selection line (LH)	2.08	−8.64	12.95	0.692
Selection line (SH)	−14.55	−24.43	−3.76	0.011*
DIC = 1,064.2				
DIC-un = 1,097.2				
Adjusted-*R* = 0.37 (0.28–0.48)*				
Sociability: model 2				
Intercept	53.595	−20.317	132.832	0.187
Selection line (LH)	−2.307	−14.649	10.95	0.71
Selection line (SH)	−15.993	−28.544	−1.834	0.019*
Fish TL (cm)	−8.974	−39.503	20.349	0.555
DIC = 742.7				
DIC-un = 768.9				
Adjusted-*R* = 0.46 (0.23–0.5)*				
Log(aggression + 1) × 10: model 1[a]				
Intercept	2.45	1.67	3.21	<0.001***
Selection line (LH)	0.15	−0.86	1.23	0.772
Selection line (SH)	−0.83	−1.93	0.20	0.13
DIC = 720.5				
DIC-un = 973.5				
Adjusted-*R* = 0.1 (0.04–0.22)^{ns}				
Log(aggression + 1) × 10: model 2[b]				
Intercept	4.61	−3.49	11.63	0.229
Selection line (LH)	0.07	−1.09	1.15	0.893
Selection line (SH)	−0.85	−2.13	0.42	0.18
Fish TL (cm)	−0.84	−3.59	2.28	0.571
DIC = 720.6				
DIC-un = 721.05				
Adjusted-*R* = 0.15 (0.05–0.28)^{ns}				

[a] Overdispersion of the model = 1.02.

[b] Overdispersion of the model = 0.92.

across ontogeny have also been reported in other fish species, such as the Eastern Mosquitofish *Gambusia holbrooki* (Polverino et al. 2016b). Similarly, in Largemouth Bass *Micropterus salmoides*, boldness was found to affect fitness differently across life stages (Ballew et al. 2017). A clear switch in boldness expressed across ontogeny has also been described in the field cricket *Gryllus integer*, for which boldness was consistently repeatable across the juvenile stage but changed considerably after maturation (Niemelä et al. 2012). Our interpretation is in accordance with a recent conceptual refinement of the pace-of-life concept (Dammhahn et al. 2018), which assumes the existence of several independent trade-offs that can be differentially shaped by ecological conditions (e.g., different size-selective mortality schedules, as in our experimental system) and stage-specific correlations of boldness and fitness (Ballew et al. 2017). Indeed, we found no change of boldness in adult females of the large-harvested line compared to controls, a result which agrees with the lack of personality changes revealed at the juvenile stage by Uusi-Heikkilä et al. (2015). This finding is noteworthy because we expected the evolution of shy individuals to be strong in the positive size-selection line following Andersen et al. (2018). Fast life histories (such as the life histories shown

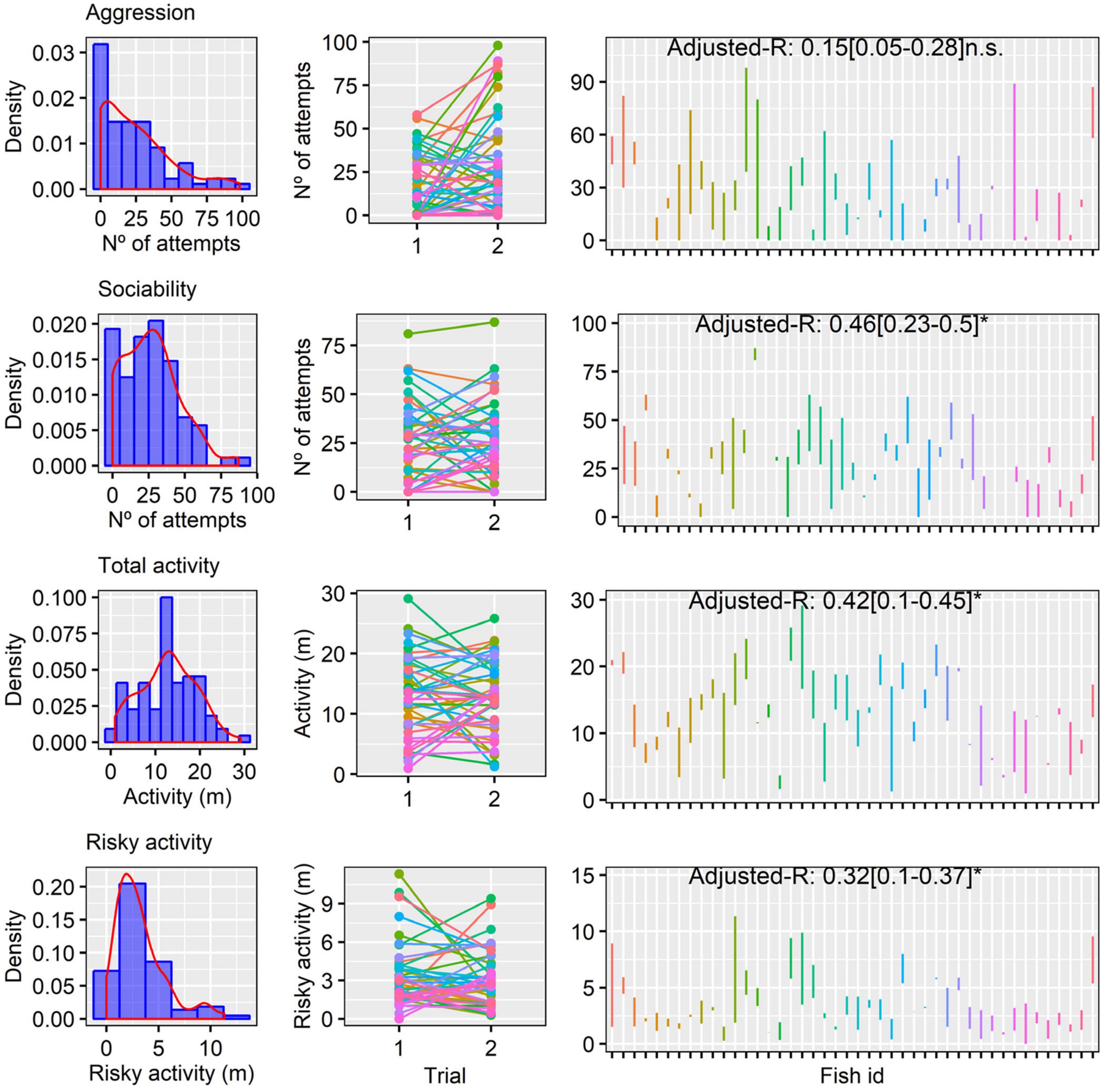

FIGURE 3. Density population plots (left column), trial individual values (middle column), and among-individual differences (right column) for each of the Zebrafish behaviors studied using model 2 (i.e., size-matched individuals were used): aggression, sociability, risky activity, and total activity. The adjusted repeatability score (adjusted-*R*; with confidence interval in brackets) and significance test results (ns = not significant; $*P < 0.05$) for each trait are shown.

by the large-harvested line) should indeed be characterized by elevated boldness (Réale et al. 2010), but the positive size-selection treatment could have created a counterforce after maturation, leading to no changes in boldness relative to the control. In particular, elevated mortality of large fish during selection in the large-harvested line could have disfavored bold phenotypes in this line because these fish grow faster through a food acquisition mechanism and thus might be more likely to be harvested (Enberg et al. 2012). In fact, during the period of size selection (F_1 to F_5), individuals were mainly fed with clumped food at the surface of the water, which can be considered a risky

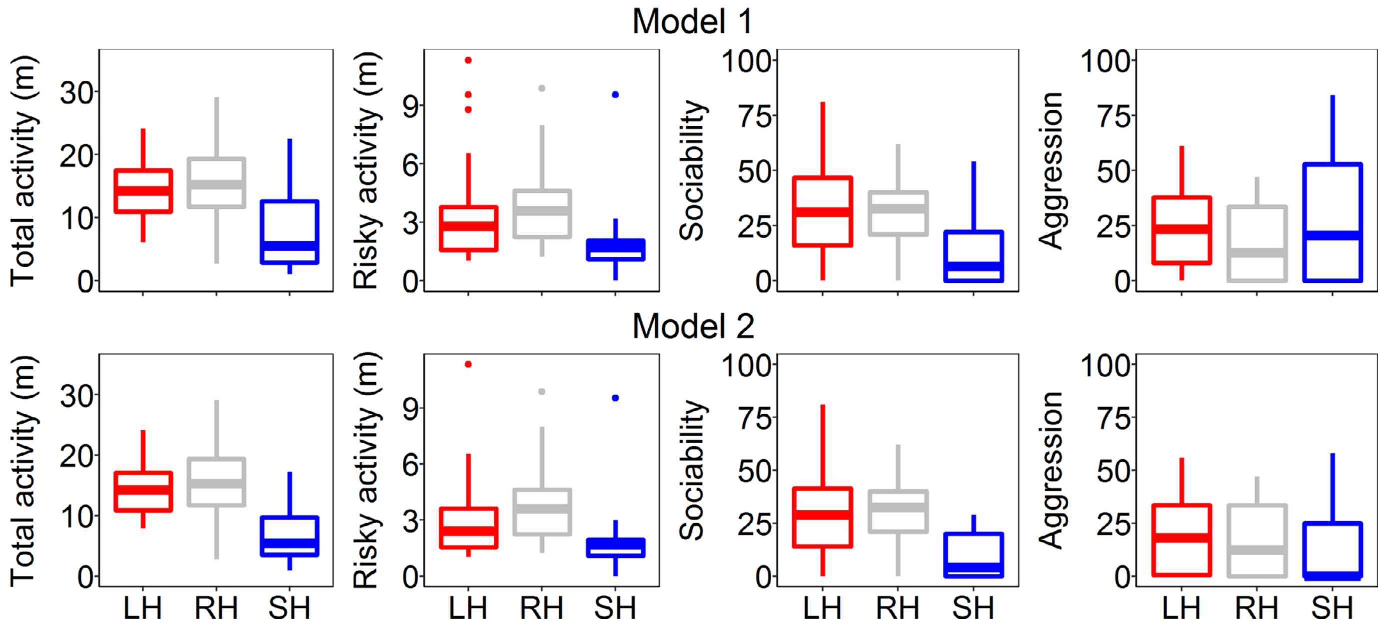

FIGURE 4. Differences among the Zebrafish selection lines in four behavioral traits (total activity [m], risky activity [m], sociability [number of attempts], and aggression [number of attempts]) among the positive (large-harvested line [LH]) and negative (small-harvested line [SH]) size-selected lines with respect to the control line (RH) that was randomly selected for size. Box plots represent the mean values across the two trials for model 1 (i.e., all individuals were used; LH: *N* = 44; RH: *N* = 36; SH: *N* = 44) and model 2 (i.e., size-matched individuals were used; LH: *N* = 30; RH: *N* = 36; SH: *N* = 22).

TABLE 3. Correlations among repeatable behaviors (total activity, risky activity, and sociability) of Zebrafish in each experimental trial (1 and 2) and model (global treatment and size-matched model) expressed as Kendall's coefficient (ns = not significant; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

	Trial 1			Trial 2		
Behavior	Total activity	Risky activity	Sociability	Total activity	Risky activity	Sociability
Model 1: global treatment model						
Total activity		0.50***	0.34***		0.52***	0.34***
Risky activity			0.21**			0.13^{ns}
Sociability						
Model 2: size-matched model						
Total activity		0.49***	0.39***		0.52***	0.37***
Risky activity			0.26*			0.23*
Sociability						

environment for Zebrafish (Spence et al. 2008). Therefore, individuals with bold personality traits could be able to grow faster by having more access to food and at the same time be disfavored under the positive size-selectivity scenario. Our work underscores that the predictions of the pace-of-life hypothesis with respect to personality and life history correlations can be context dependent and can vary among ecological conditions, thereby complicating generalizations (Polverino et al. 2018; Royauté et al. 2018; Wright et al. 2018). In fact, our results suggest that positive and negative size-selective mortality create diverse evolutionary pressures triggering boldness outcomes that cannot be easily predicted with a simple correlation framework between fast/slow life history and bold/shy personality traits (Claireaux et al. 2018).

An alternative explanation for our results relates to the fact that we measured boldness of a social fish during individual experimental trials. Isolation creates physiological stress in Zebrafish (Forsatkar et al. 2017), which can lead to outcomes that do not represent what a particular fish would express in a group or in less-stressful situations (Killen et al. 2013). Moreover, the mean individual-level personality traits that we measured might not necessarily correspond with the collective phenotype exhibited by shoals of Zebrafish as in the original selection environment. For example, Jolles et al. (2017) found that Threespine Sticklebacks *Gasterosteus aculeatus* showing high levels of proximity to confined shoals in an individual social preference test displayed weak social interactions and polarization when in shoals. Therefore, it is conceivable that in a social context, the selection lines could display a different level of boldness and also a different level of activity and sociability compared to when tested individually. Preliminary results of ongoing experiments conducted by our group indeed suggest that when in mixed-sex shoals, the small-harvested Zebrafish take collectively more risks than control fish (Figure S2), while the large-harvested fish do not differ from the control. These initial findings suggest that one must be cautious with classical personality tests of focal individuals when the actual selection environment is a social setting, as was the case in our harvesting experiment. Therefore, future work on the FIE of personality traits should focus on individual personality traits expressed in a group context and across ontogeny, particularly because given that many fish species form shoals (Pitcher 1986), the phenotypes expressed in a social environment represent the ecologically relevant outcome of adaptation to natural and fisheries-induced selection pressures.

A last possible explanation could be related to the fact that in Zebrafish, as in other small-bodied species, larger individuals could be subject to stronger natural predation risk than small ones (Brown and Braithwaite 2004; Polverino et al. 2016a) because they offer more energy to gape-limited predators than smaller individuals (Persson et al. 2003). Genotypes that are programmed for investing into somatic instead of gonadal growth are able to attain larger maximum size (e.g., as in the individuals of the small-harvested line; Uusi-Heikkilä et al. 2015). As such, taking less risk could be a strategy for avoiding predation in favor of future reproduction. Indeed, Polverino et al. (2016a) demonstrated that larger Zebrafish of the same cohort were less active and less risk prone in a potentially dangerous open field. We can exclude that the changes in boldness observed in our study were due to a correlated response to differences in body length among selection lines. Instead, we conclude that the lower average boldness of the small-harvested line represented an evolutionary response by the intrinsically larger-growing individuals to negative size-selective mortality. We propose that this response can be explained, at least in part, by the fitness benefit of more cautious behaviour in relation to natural predators by larger-sized Zebrafish—a behavioral strategy that appears more common in the small-harvested line compared to the control.

Despite the possibility that total activity and risky activity could be measures of the same latent personality trait (i.e., boldness), it is also possible that they represent the same latent measures of total activity or, alternatively, that total activity represents a separate personality trait that is merely correlated with boldness (Reale et al. 2007). In both cases, the fact that we found lower activity in the small-harvested line compared to the control line suggests that a mechanism related to conserving energy could be at play. Swimming produces energetic costs in fishes (Kitchell et al. 1977), and individuals that swim less might allocate energy surpluses more efficiently to somatic growth (Enberg et al. 2012). Such a mechanism could explain why the small-harvested line, which evolved a larger terminal size than the large-harvested line, evolved a lower average level of activity compared to the control line when focal fish were assayed individually.

Our work constitutes the first empirical test of two recent theoretical life history models of the FIE of boldness (Andersen et al. 2018; Claireaux et al. 2018). Andersen et al. (2018) predicted the evolution of shy individuals when fishing mortality is directed exclusively at large adult fish and the evolution of bold individuals when fishing mortality also or mainly captures juveniles. Our work only partially supported these predictions. We did not directly determine the degree to which our size-selection treatments captured adults versus juveniles, but in all likelihood, fishing mortality in the large-harvested treatment could have been more adult-oriented than fishing mortality in the small-harvested treatment. It is important to consider that the size-selective harvesting occurred when 50% of the individuals belonging to the control line were mature (Uusi-Heikkilä et al. 2015). All fish that survived the size-selective harvesting were then allowed to mature and contribute to the next generation. Earlier results reported rapid evolution of smaller size and younger age at maturation in both size-selected lines relative to controls (Uusi-Heikkilä et al. 2015). This finding suggests that the timing of harvest (i.e., when 50% of the control line was mature) could have created a condition whereby size selection targeted mainly (negative size selection) or exclusively (positive size selection) adults in both size-selection treatments and that these effects were reinforced over generations as maturation continued to shift toward smaller sizes and younger ages. Assuming that only body size determines the harvest probability (i.e., without other covarying behavioral traits, which appears somewhat unlikely in the wild; Arlinghaus et al. 2017), the model by Andersen et al. (2018) suggests that the evolution of shy individuals should occur in both size selection treatments. We found evidence for the evolution of shy individuals in the small-harvested line but not in the large-harvested line. However, this result for the large-harvested adults still agrees with previous findings for juveniles of the same line (Uusi-Heikkilä et al. 2015).

Sociability

The negative size-selection treatment resulted in evolutionary changes in the sociability of adult female Zebrafish—a trait that has received only cursory treatment so far in the literature on fisheries-induced selection and evolution (but see Hollins et al. 2018; Louison et al. 2018; Thambithurai et al. 2018). We predicted that the large- and small-harvested females would evolve higher and lower sociability than control females, respectively. Only the latter prediction was supported by our results: the small-harvested line evolved lower average sociability compared to the control line, while no changes were revealed in the large-harvested line. The small-harvested treatment could have favored low sociability because reduced social interaction would likely lead to increased consumption during the clumped and, hence, scramble-competitive feeding environment that was presented in the original harvest experiment (Uusi-Heikkilä et al. 2015). As mentioned above, individual-assayed social personalities could result in different phenotypic outcomes at the group level (e.g., Jolles et al. 2017), and preliminary results of our research group indeed support the notion that the small-harvested line forms tighter shoals than the control line when assayed in groups (Figure S2). This is noteworthy because shoaling behavior facilitates foraging efficiency in Zebrafish (Nunes et al. 2017). Thus, less-social small-harvested individuals may have attained larger sizes during the harvesting experiment because individually asocial personality traits might collectively lead to more cohesive groups, but this assumption necessitates a proper future test on the group differences of large- and small-harvested fish relative to control fish. Moreover, we need to better understand how the fish shoals of the different lines use the surface of the water, which is the area where feeding occurred during size selection. An alternative interpretation could be that what we measured in the sociability test (attempts of the focal fish to join the shoal) is in fact indicative of boldness (e.g., Moretz et al. 2007; Roy et al. 2017). However, the sociability trait was more tightly correlated to total activity than to risky activity, suggesting that this interpretation is unlikely.

Limitations and Further Study

We provide the first experimental evidence on how size-selective harvesting may trigger the evolution of fish activity, boldness, and sociability in a social species. However, our study has a number of limitations. First, our results were confined to females. Given that Zebrafish males and females can display different behaviors (Spence et al. 2008), our findings cannot be generalized to males. Second, in our sociability test, we used a shoaling stimulus composed of Zebrafish from the control line. It is possible that the subpopulations evolved preferences for their own line (Engeszer et al. 2007), which could have affected our results. Third, we did not measure the evolution of personality using a longitudinal approach (i.e., measuring the same individual at different ages); thus, our inferred explanation that maturation reversed personality in the small-harvested line remains speculative. Finally, we may have overlooked important behaviors that relate to growth variation and that might have changed together with size selection. For example, rank in dominance hierarchies determines food monopolization in Zebrafish (Hamilton and Dill 2002). In fact, during a separate experiment with the same selection lines at F_{11} (Figure S3), we detected a significant difference in dyadic agonistic interactions (i.e., bites) among the selection lines using size-matched males and females (Figure S3). The results indicate that the small-harvested line displayed more agonistic interactions than the control line. This suggests that other behavioral traits not measured in the present study might differ among the selection lines, indicating a need for further research. One of the key dimensions that require study is how Zebrafish groups use vertical space and, in particular, the surface of the water column, which is not only risky (e.g., exposure to avian predators) but also profitable for feeding (at least in the harvesting experiment as conducted here). These and other traits should be studied in groups rather than individuals to better measure phenotypes in the original environment on which the selection experiment operated.

Conclusions

We demonstrated that five generations of size selection in Zebrafish induced evolutionary changes in individual-level personality in females but did so in unexpected ways, and the changes were inconsistent with respect to the negative or positive size-selection treatments. Our results suggest that positive size selection may not alter average individual personality, while negative size selection has left a legacy in relation to activity, boldness, and sociability. Clearly, our results must be interpreted with caution and may not translate directly to real-world fishing scenarios, where the fish live in groups, have multiple spawning events, and/or have overlapping generations. Furthermore, behavior might be under direct selection by fisheries, but in our experiment, selection was strictly based on size. Nevertheless, at a broad level, our work suggests that exclusively size-selective harvesting has the potential to alter the evolution of personality traits within just five generations and that such effects are maintained for a further five generations after harvesting is stopped. In that sense, our findings support recent theoretical work predicting how elevated, size-selective, and behavior-selective fishing evolutionarily alters boldness and other personality traits (Andersen et al. 2018; Claireaux et al. 2018). Fisheries-induced evolution of personality traits can have consequences for social groups, populations, food webs, and fisheries and thus demands careful empirical study (Arlinghaus et al. 2017; Diaz Pauli and Sih 2017).

ACKNOWLEDGMENTS

V.S. was supported by a Leibniz–DAAD (German Academic Exchange Service) postdoctoral research fellowship (Number 91632699). We are grateful to Benjamin Laschinski for his help during an initial phase of this project and the collection of experimental videos. J.A. was supported by a Juan de la Cierva post-doctoral grant funded by the Spanish Ministry of Economy, Industry, and Competitiveness (IJCI-2016-27681). C.D.-G. was funded by a fellowship from the Spanish National Institute for Agricultural and Food Research and Technology. S.U.H. was funded by the Finnish Cultural Foundation. A.E.H. was supported by a University of Minnesota Doctoral Dissertation Fellowship. We thank the reviewers for thoughtful feedback that improved our manuscript. R.A., S.U.H., and A.D.M.W. conceived the experiment. V.S., K.F., C.T.M., and C.D.-G. conducted the experiment and behavioral analysis. V.S., J.A., and A.E.H. performed statistical analyses. V.S. and R.A. mainly interpreted the results and wrote the manuscript, with feedback from all other authors. There is no conflict of interest declared in this article.

ORCID

Valerio Sbragaglia https://orcid.org/0000-0002-4775-7049
Robert Arlinghaus https://orcid.org/0000-0003-2861-527X

REFERENCES

Ahrens, R. N., C. J. Walters, and V. Christensen. 2012. Foraging arena theory. Fish and Fisheries 13:41–59.

Alós, J., M. Martorell-Barceló, and A. Campos-Candela. 2017. Repeatability of circadian behavioural variation revealed in free-ranging marine fish. Royal Society Open Science 4(2):160791.

Alós, J., M. Palmer, R. Rosselló, and R. Arlinghaus. 2016. Fast and behavior-selective exploitation of a marine fish targeted by anglers. Scientific Reports 6:38093.

Andersen, K. H., L. Marty, and R. Arlinghaus. 2018. Evolution of boldness and life history in response to selective harvesting. Canadian Journal of Fisheries and Aquatic Sciences 75:271–281.

Ariyomo, T. O., M. Carter, and P. J. Watt. 2013. Heritability of boldness and aggressiveness in the Zebrafish. Behavior Genetics 43:161–167.

Ariyomo, T. O., and P. J. Watt. 2012. The effect of variation in boldness and aggressiveness on the reproductive success of Zebrafish. Animal Behaviour 83:41–46.

Arlinghaus, R., K. L. Laskowski, J. Alós, T. Klefoth, C. T. Monk, S. Nakayama, and A. Schröder. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. Fish and Fisheries 18:360–373.

Ballew, N. G., G. G. Mittelbach, and K. T. Scribner. 2017. Fitness consequences of boldness in juvenile and adult Largemouth Bass. American Naturalist 189:396–406.

Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour 77:771–783.

Bernardo, J. 1993. Determinants of maturation in animals. Trends in Ecology and Evolution 8:166–173.

Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences of the USA 105:2919–2922.

Biro, P. A., and P. Sampson. 2015. Fishing directly selects on growth rate via behaviour: implications of growth-selection that is independent of size. Proceedings of the Royal Society B: Biological Sciences 282:20142283.

Brown, C., and V. A. Braithwaite. 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. Animal Behaviour 68:1325–1329.

Brown, C. J., A. J. Hobday, P. E. Ziegler, and D. C. Welsford. 2008. Darwinian fisheries science needs to consider realistic fishing pressures over evolutionary time scales. Marine Ecology Progress Series 369:257–266.

Claireaux, M., C. Jørgensen, and K. Enberg. 2018. Evolutionary effects of fishing gear on foraging behavior and life-history traits. Ecology and Evolution 8:10711–10721.

Conover, D. O., S. B. Munch, and S. A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. Proceedings of the Royal Society B: Biological Sciences 276:2015–2020.

Conrad, J. L., K. L. Weinersmith, T. Brodin, J. B. Saltz, and A. Sih. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. Journal of Fish Biology 78:395–435.

Dahlbom, S. J., D. Lagman, K. Lundstedt-Enkel, L. F. Sundström, and S. Winberg. 2011. Boldness predicts social status in Zebrafish (*Danio rerio*). PLoS ONE [online serial] 6:e23565.

Dammhahn, M., N. J. Dingemanse, P. T. Niemelä, and D. Réale. 2018. Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. Behavioral Ecology and Sociobiology 72:62.

Devine, J. A., P. J. Wright, H. E. Pardoe, and M. Heino. 2012. Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 69:1105–1120.

Diaz Pauli, B., and M. Heino. 2014. What can selection experiments teach us about fisheries-induced evolution? Biological Journal of the Linnean Society 111:485–503.

Diaz Pauli, B., and A. Sih. 2017. Behavioural responses to human-induced change: why fishing should not be ignored. Evolutionary Applications 10:231–240.

Diaz Pauli, B., M. Wiech, M. Heino, and A. C. Utne-Palm. 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated Guppy *Poecilia reticulata* fishery. Journal of Fish Biology 86:1030–1045.

Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. Journal of Animal Ecology 82:39–54.

DiRienzo, N., J. N. Pruitt, and A. V. Hedrick. 2012. Juvenile exposure to acoustic sexual signals from conspecifics alters growth trajectory and an adult personality trait. Animal Behaviour 84:861–868.

Dochtermann, N. A., T. Schwab, and A. Sih. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. Proceedings of the Royal Society B: Biological Sciences 282:20142201.

Dunlop, E. S., A. M. Eikeset, and N. C. Stenseth. 2015. From genes to populations: how fisheries-induced evolution alters stock productivity. Ecological Applications 25:1860–1868.

Eikeset, A. M., E. S. Dunlop, M. Heino, G. Storvik, N. C. Stenseth, and U. Dieckmann. 2016. Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. Proceedings of the National Academy of Sciences of the USA 113:15030–15035.

Enberg, K., C. Jørgensen, E. S. Dunlop, Ø. Varpe, D. S. Boukal, L. Baulier, S. Eliassen, and M. Heino. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Marine Ecology 331:1–25.

Engeszer, R. E., L. A. Da Barbiano, M. J. Ryan, and D. M. Parichy. 2007. Timing and plasticity of shoaling behaviour in the Zebrafish, *Danio rerio*. Animal Behaviour 74:1269–1275.

Forsatkar, M. N., O. Safari, and C. Boiti. 2017. Effects of social isolation on growth, stress response, and immunity of Zebrafish. Acta Ethologica 20:255–261.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Gerlai, R., M. Lahav, S. Guo, and A. Rosenthal. 2000. Drinks like a fish: Zebra fish (*Danio rerio*) as a behavior genetic model to study alcohol effects. Pharmacology Biochemistry and Behavior 67:773–782.

Gíslason, D., R. L. McLaughlin, B. W. Robinson, A. Cook, and E. S. Dunlop. 2018. Rapid changes in age and size at maturity in Lake Erie Yellow Perch (*Perca flavescens*) are not explained by harvest. Canadian Journal of Fisheries and Aquatic Sciences 75:211–223.

Gyuris, E., O. Feró, and Z. Barta. 2012. Personality traits across ontogeny in firebugs, *Pyrrhocoris apterus*. Animal Behaviour 84:103–109.

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Hämäläinen, A., E. Immonen, M. Tarka, and W. Schuett. 2018. Evolution of sex-specific pace-of-life syndromes: causes and consequences. Behavioral Ecology and Sociobiology 72:50.

Hamilton, I. M., and L. M. Dill. 2002. Monopolization of food by Zebrafish (*Danio rerio*) increases in risky habitats. Canadian Journal of Zoology 80:2164–2169.

Härkönen, L., P. Hyvärinen, J. Paappanen, and A. Vainikka. 2014. Explorative behavior increases vulnerability to angling in hatchery-reared Brown Trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 71:1900–1909.

Harrison, P. M., L. F. G. Gutowsky, E. G. Martins, D. A. Patterson, S. J. Cooke, and M. Power. 2014. Personality-dependent spatial ecology occurs independently from dispersal in wild Burbot (*Lota lota*). Behavioral Ecology 26:483–492.

Heino, M., B. Díaz Pauli, and U. Dieckmann. 2015. Fisheries-induced evolution. Annual Review of Ecology, Evolution, and Systematics 46:461–480.

Heino, M., and O. R. Godø. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science 70:639–656.

Hollins, J., D. Thambithurai, B. Koeck, A. Crespel, D. M. Bailey, S. J. Cooke, J. Lindström, K. J. Parsons, and S. S. Killen. 2018. A physiological perspective on fisheries-induced evolution. Evolutionary Applications 11:561–576.

Januchowski-Hartley, F. A., N. A. J. Graham, D. A. Feary, T. Morove, and J. E. Cinner. 2011. Fear of fishers: human predation explains behavioral changes in coral reef fishes. PLoS ONE [online serial] 6: e22761.

Jolles, J. W., N. J. Boogert, V. H. Sridhar, I. D. Couzin, and A. Manica. 2017. Consistent individual differences drive collective behavior and group functioning of schooling fish. Current Biology 27:2862–2868.

Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. G. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp. 2007. Ecology: managing evolving fish stocks. Science 318:1247–1248.

Jørgensen, C., and R. E. Holt. 2013. Natural mortality: its ecology, how it shapes fish life histories, and why it may be increased by fishing. Journal of Sea Research 75:8–18.

Kalueff, A. V., M. Gebhart, A. M. Stewart, J. M. Cachat, M. Brimmer, J. S. Chawla, C. Craddock, E. J. Kyzar, A. Roth, S. Landsman, S. Gaikwad, K. Robinson, E. Baatrup, K. Tierney, A. Shamchuk, W. Norton, N. Miller, T. Nicolson, O. Braubach, C. P. Gilman, J. Pittman, D. B. Rosemberg, R. Gerlai, D. Echevarria, E. Lamb, S. C. F. Neuhauss, W. Weng, L. Bally-Cuif, and H. Schneider. 2013. Towards a comprehensive catalog of Zebrafish behavior 1.0 and beyond. Zebrafish 10:70–86.

Kekäläinen, J., T. Podgorniak, T. Puolakka, P. Hyvärinen, and A. Vainikka. 2014. Individually assessed boldness predicts *Perca fluviatilis* behaviour in shoals, but is not associated with the capture order or angling method. Journal of Fish Biology 85:1603–1616.

Killen, S. S., S. Marras, N. B. Metcalfe, D. J. McKenzie, and P. Domenici. 2013. Environmental stressors alter relationships between physiology and behaviour. Trends in Ecology and Evolution 28:651–658.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34:1922–1935.

Klefoth, T., T. Pieterek, and R. Arlinghaus. 2013. Impacts of domestication on angling vulnerability of Common Carp, *Cyprinus carpio*: the role of learning, foraging behaviour and food preferences. Fisheries Management and Ecology 20:174–186.

Klefoth, T., C. Skov, A. Kuparinen, and R. Arlinghaus. 2017. Toward a mechanistic understanding of vulnerability to hook-and-line fishing: boldness as the basic target of angling-induced selection. Evolutionary Applications 10:994–1006.

Kuparinen, A., S. Kuikka, and J. Merilä. 2009. Estimating fisheries-induced selection: traditional gear selectivity research meets fisheries-induced evolution. Evolutionary Applications 2:234–243.

Larson, E. T., D. M. O'Malley, and R. H. Melloni Jr. 2006. Aggression and vasotocin are associated with dominant–subordinate relationships in Zebrafish. Behavioural Brain Research 167:94–102.

Laugen, A. T., G. H. Engelhard, R. Whitlock, R. Arlinghaus, D. J. Dankel, E. S. Dunlop, A. M. Eikeset, K. Enberg, C. Jørgensen, S. Matsumura, S. Nusslé, D. Urbach, L. Baulier, D. S. Boukal, B. Ernande, F. D. Johnston, F. Mollet, H. Pardoe, N. O. Therkildsen, S. Uusi-Heikkilä, A. Vainikka, M. Heino, A. D. Rijnsdorp, and U. Dieckmann. 2014. Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. Fish and Fisheries 15:65–96.

Li, C.-Y., C. Curtis, and R. L. Earley. 2018. Nonreversing mirrors elicit behaviour that more accurately predicts performance against live opponents. Animal Behaviour 137:95–105.

Louison, M. J., J. D. Jeffrey, C. D. Suski, and J. A. Stein. 2018. Sociable Bluegill, *Lepomis macrochirus*, are selectively captured via recreational angling. Animal Behaviour 142:129–137.

McPeek, M. A. 2004. The growth/predation risk trade-off: so what is the mechanism? American Naturalist 163:E88–E111.

Mittelbach, G. G., N. G. Ballew, and M. K. Kjelvik. 2014. Fish behavioral types and their ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 71:927–944.

Monk, C. T., and R. Arlinghaus. 2017. Eurasian Perch, *Perca fluviatilis*, spatial behaviour determines vulnerability independent of angler skill in a whole-lake reality mining experiment. Canadian Journal of Fisheries and Aquatic Sciences 75:417–428.

Moretz, J. A., E. P. Martins, and B. D. Robison. 2007. Behavioral syndromes and the evolution of correlated behavior in Zebrafish. Behavioral Ecology 18:556–562.

Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.

Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biological Reviews 85:935–956.

Niemelä, P. T., A. Vainikka, A. V. Hedrick, and R. Kortet. 2012. Integrating behaviour with life history: boldness of the field cricket, *Gryllus integer*, during ontogeny. Functional Ecology 26:450–456.

Nunes, A. R., N. Ruhl, S. Winberg, and R. F. Oliveira. 2017. Social phenotypes in Zebrafish. Pages 95–130 *in* A. V. Kalueff, editor. The rights and wrongs of Zebrafish: behavioral phenotyping of Zebrafish. Springer International Publishing, Cham, Switzerland.

Özbilgin, H., and C. W. Glass. 2004. Role of learning in mesh penetration behaviour of Haddock (*Melanogrammus aeglefinus*). ICES Journal of Marine Science 61:1190–1194.

Palkovacs, E. P., M. T. Kinnison, C. Correa, C. M. Dalton, and A. P. Hendry. 2012. Fates beyond traits: ecological consequences of human-induced trait change. Evolutionary Applications 5:183–191.

Palkovacs, E. P., M. M. Moritsch, G. M. Contolini, and F. Pelletier. 2018. Ecology of harvest-driven trait changes and implications for ecosystem management. Frontiers in Ecology and the Environment 16:20–28.

Persson, L., A. M. De Roos, D. Claessen, P. Byström, J. Lövgren, S. Sjögren, R. Svanbäck, E. Wahlström, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proceedings of the National Academy of Sciences 100:4035–4039.

Pham, M., J. Raymond, J. Hester, E. Kyzar, S. Gaikwad, I. Bruce, C. Fryar, S. Chanin, J. Enriquez, S. Bagawandoss, I. Zapolsky, J. Green, A. M. Stewart, B. D. Robison, and A. V. Kalueff. 2012. Assessing social behavior phenotypes in adult Zebrafish: shoaling, social preference, and mirror biting tests. Pages 231–246 *in* A. V. Kalueff and A. M. Stewart, editors. Zebrafish protocols for neurobehavioral research. Humana Press, New York.

Philipp, D. P., S. J. Cooke, J. E. Claussen, J. B. Koppelman, C. D. Suski, and D. P. Burkett. 2009. Selection for vulnerability to angling in Largemouth Bass. Transactions of the American Fisheries Society 138:189–199.

Pierce, R. B. 2010. Long-term evaluations of length limit regulations for Northern Pike in Minnesota. North American Journal of Fisheries Management 30:412–432.

Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. Pages 294–337 *in* T. J. Pitcher, editors. The behaviour of teleost fishes. Springer, Berlin.

Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6:7–11.

Polverino, G., D. Bierbach, S. S. Killen, S. Uusi-Heikkila, and R. Arlinghaus. 2016a. Body length rather than routine metabolic rate and body condition correlates with activity and risk-taking in juvenile Zebrafish *Danio rerio*. Journal of Fish Biology 89:2251–2267.

Polverino, G., C. Cigliano, S. Nakayama, and T. Mehner. 2016b. Emergence and development of personality over the ontogeny of fish in absence of environmental stress factors. Behavioral Ecology and Sociobiology 70:2027–2037.

Polverino, G., F. Santostefano, C. Díaz-Gil, and T. Mehner. 2018. Ecological conditions drive pace-of-life syndromes by shaping relationships between life history, physiology and behaviour in two populations of Eastern Mosquitofish. Scientific Reports 8:14673.

Raat, A. J. P.. 1985. Analysis of angling vulnerability of Common Carp, *Cyprinus carpio* L., in catch-and-release angling in ponds. Aquaculture Research 16:171–187.

Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:4051–4063.

Reale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews of the Cambridge Philosophical Society 82:291–318.

Roy, T., R. Shukla, and A. Bhat. 2017. Risk-taking during feeding: between-and within-population variation and repeatability across contexts among wild Zebrafish. Zebrafish 14:393–403.

Royauté, R., M. A. Berdal, C. R. Garrison, and N. A. Dochtermann. 2018. Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. Behavioral Ecology and Sociobiology 72:64.

Rudstam, L. G., J. J. Magnuson, and W. M. Tonn. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Canadian Journal of Fisheries and Aquatic Sciences 41:1252–1255.

Salinas, S., K. O. Perez, T. A. Duffy, S. J. Sabatino, L. A. Hice, S. B. Munch, and D. O. Conover. 2012. The response of correlated traits following cessation of fishery-induced selection. Evolutionary Applications 5:657–663.

Sbragaglia, V., L. Morroni, L. Bramanti, B. Weitzmann, R. Arlinghaus, and E. Azzurro. 2018. Spearfishing modulates flight initiation distance of fishes: the effects of protection, individual size, and bearing a speargun. ICES Journal of Marine Science 75:1779–1789.

Sharpe, D. M. T., and A. P. Hendry. 2009. Synthesis: life history change in commercially exploited fish stocks: an analysis of trends across studies. Evolutionary Applications 2:260–275.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology and Evolution 19:372–378.

Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19:448–455.

Spence, R., G. Gerlach, C. Lawrence, and C. Smith. 2008. The behaviour and ecology of the Zebrafish, *Danio rerio*. Biological Reviews of the Cambridge Philosophical Society 83:13–34.

Stamps, J. A. 2007. Growth–mortality tradeoffs and "personality traits" in animals. Ecology Letters 10:355–363.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Stewart, A. M., S. Gaikwad, E. Kyzar, and A. V. Kalueff. 2012. Understanding spatio-temporal strategies of adult Zebrafish exploration in the open field test. Brain Research 1451(Supplement C):44–52.

Stirling, D. G., D. Réale, and D. A. Roff. 2002. Selection, structure and the heritability of behaviour. Journal of Evolutionary Biology 15: 277–289.

Sutter, D. A. H., C. D. Suski, D. P. Phillipp, T. Klefoth, D. H. Wahl, P. Kersten, S. J. Cooke, and R. Arlinghaus. 2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proceedings of the National Academy of Sciences 109:20960–20965.

Thambithurai, D., J. Hollins, T. Van Leeuwen, A. Rácz, J. Lindström, K. Parsons, and S. S. Killen. 2018. Shoal size as a key determinant of vulnerability to capture under a simulated fishery scenario. Ecology and Evolution 8:6505–6514.

Toms, C. N., and D. J. Echevarria. 2014. Back to basics: searching for a comprehensive framework for exploring individual differences in Zebrafish (*Danio rerio*) behavior. Zebrafish 11:325–340.

Uusi-Heikkilä, S., K. Lindström, N. Parre, R. Arlinghaus, J. Alós, and A. Kuparinen. 2016. Altered trait variability in response to size-selective mortality. Biology Letters 12(9):20160584.

Uusi-Heikkilä, S., T. Savilammi, E. Leder, R. Arlinghaus, and C. R. Primmer. 2017. Rapid, broad-scale gene expression evolution in experimentally harvested fish populations. Molecular Ecology 26:3954–3967.

Uusi-Heikkilä, S., A. R. Whiteley, A. Kuparinen, S. Matsumura, P. A. Venturelli, C. Wolter, J. Slate, C. R. Primmer, T. Meinelt, S. S. Killen, D. Bierbach, G. Polverino, A. Ludwig, and R. Arlinghaus. 2015. The evolutionary legacy of size-selective harvesting extends from genes to populations. Evolutionary Applications 8:597–620.

Uusi-Heikkilä, S., C. Wolter, T. Klefoth, and R. Arlinghaus. 2008. A behavioral perspective on fishing-induced evolution. Trends in Ecology and Evolution 23:419–421.

Vainikka, A., I. Tammela, and P. Hyvärinen. 2016. Does boldness explain vulnerability to angling in Eurasian Perch *Perca fluviatilis*? Current Zoology 62:109–115.

van Wijk, S. J., M. I. Taylor, S. Creer, C. Dreyer, F. M. Rodrigues, I. W. Ramnarine, C. van Oosterhout, and G. R. Carvalho. 2013. Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. Frontiers in Ecology and the Environment 11:181–187.

Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters 9:142–148.

Ward, T. D., D. A. Algera, A. J. Gallagher, E. Hawkins, A. Horodysky, C. Jørgensen, S. S. Killen, D. J. McKenzie, J. D. Metcalfe, M. A. Peck, M. Vu, and S. J. Cooke. 2016. Understanding the individual to implement the ecosystem approach to fisheries management. Conservation Physiology 4:cow005.

Way, G. P., N. Ruhl, J. L. Snekser, A. L. Kiesel, and S. P. McRobert. 2015. A comparison of methodologies to test aggression in Zebrafish. Zebrafish 12:144–151.

Wilson, A. D. M., T. R. Binder, K. P. McGrath, S. J. Cooke, and J.-G. J. Godin. 2011. Capture technique and fish personality: angling targets timid Bluegill Sunfish, *Lepomis macrochirus*. Canadian Journal of Fisheries and Aquatic Sciences 68:749–757.

Wilson, A. D. M., J. W. Brownscombe, B. Sullivan, S. Jain-Schlaepfer, and S. J. Cooke. 2015. Does angling technique selectively target fishes based on their behavioural type? PLoS ONE [online serial] 10:e0135848.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology and Evolution 27:452–461.

Wright, J., G. H. Bolstad, Y. G. Araya-Ajoy, and N. J. Dingemanse. 2018. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. Biological Reviews of the Cambridge Philosophical Society 94:230–247.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.