

**Title:** Size-selective harvesting and individual personality in a social fish

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## ABSTRACT

In fisheries worldwide, larger fish are subjected to substantially greater fishing mortality than smaller fish. Body length and behavioral traits are often correlated, such that fisheries-induced changes in either behaviour or morphology can also alter other traits as result of direct or indirect selection. Consistent behavioral differences among individuals, known as personality traits, provide the proximate framework by which selection can act; however, empirical evidence regarding how size-selective harvesting alters mean personality traits in exploited stocks is scarce. We examined three experimental lines of zebrafish (*Danio rerio*) that were exposed to positive, negative or random size-selective harvest over five generations to investigate whether simulated fishing changed the mean personality of the survivors five generations after harvesting was halted. We found that females mean boldness (defined as risk-taking tendency), activity and sociability were significantly altered relative to a randomly harvested line; however, harvest-induced changes in personality were only detected in the negatively size-selected line, in which 75% of the smallest fishes were harvested. By contrast, we did not find evidence for harvest-induced evolution of personality in the positively size-selected line, in which 75% of the largest fishes were harvested. We conclude that size-selective harvesting alters individual fish personality in a social fish.

## INTRODUCTION

In most fish stocks, fishing mortality on adults is substantially larger than natural mortality (Brown et al. 2008). Therefore, fishing has the potential to alter selection pressures relative to natural conditions (Heino et al. 2015; Jørgensen et al. 2007; Law 2000). In addition, most fishing gears preferentially catch the largest individuals of a population, i.e., they operate in a positively size-selective fashion (Jørgensen et al. 2007; Kuparinen et al. 2009). Such selection can lead to life-history adaptations and favor the evolution of a fast life-history (Jørgensen et al. 2007). Fisheries do, however, not always preferentially harvest the largest members of a population. In fact, some fishing techniques show alternative selectivity patterns in relation to size, e.g., dome shaped selectivity in gill net fisheries (Kuparinen et al. 2009). Moreover, in recreational fisheries, harvest regulations such as maximum-length limits can provide protection to the largest individuals in a population (Pierce 2010). Thus, the actual size-selectivity of a fishery is the outcome of the gear's selectivity pattern combined with the harvest regulation in place. Body size is a fundamental property in the structuring of aquatic communities (de Roos and Persson 2013; Ebenman and Persson 2012). Thus, selection on body size and the resulting demographic and/or evolutionary changes of body size in exploited populations are likely to exert relevant effects on population dynamics (Ebenman and Persson 2012; Uusi-Heikkilä et al. 2015), with the potential to also affect food webs and ecosystems (Kuparinen et al. 2016; Palkovacs et al. 2018).

Intense harvest in both unselective and positively size-selective scenarios has been found to generally (but not necessarily, Dunlop et al. 2015; Gíslason et al. 2017) select for fast life-histories within just a few generations (Heino et al. 2015; Jørgensen et al. 2007; Laugen et al. 2014; Uusi-Heikkilä et al. 2015; van Wijk et al. 2013). Fast life-

histories are characterized by fast juvenile growth, early maturation at small size and elevated reproductive investment, which collectively reduce post maturation growth and terminal length (Jørgensen et al. 2007). Most research on fisheries-induced evolution (FIE) has focused on life-history adaptations (Devine et al. 2012; Sharpe and Hendry 2009), with much less attention devoted to the evolution of behavioral and physiological traits (Arlinghaus et al. 2017; Heino et al. 2015; Heino and Godø 2002; Hollins et al. 2018; Uusi-Heikkilä et al. 2008). Changes in life-history traits can indirectly alter behavior because life-history traits (e.g., growth rate, size at maturation, reproductive effort) are often correlated with behaviors expressed by individual fish (Biro and Stamps 2010; Réale et al. 2010; Wolf et al. 2007). Behavioral traits can also be under direct selection through a co-variance of behavior and vulnerability to fishing gear and can thus change in direct response to fishing-induced selection (e.g., Biro and Post 2008; Biro and Sampson 2015; Klefoth et al. 2017; Monk and Arlinghaus 2017).

Behavioral changes in exploited fish stocks may be plastic (e.g., hook avoidance learning or due to relaxation of density-dependence) as well as genetic (Alós et al. 2015; Allendorf and Hard 2009; Arlinghaus et al. 2017; Tsuboi et al. 2016). Plastically, fish have been found to react strongly to fishing exposure, usually displaying increased shyness and decreased exploration towards certain gear, such as baited hooks (Arlinghaus et al. 2017). Adaptive responses have been observed after exposure to a variety of fishing gears, including nets (e.g., Özbilgin and Glass 2004), hook-and-line angling (e.g., Klefoth et al. 2013; Raat 1985) and spearfishing (e.g., Januchowski-Hartley et al. 2011; Sbragaglia et al. 2018).

Fisheries-induced evolutionary changes in behavior can happen additionally via at least three potentially coexisting mechanisms. First, as mentioned above, harvesting

often favors fast life-histories, which can be expected to favor bold individuals that forage intensively and/or aggressively to reap fitness benefits early in life (Andersen et al. 2018; Jørgensen and Holt 2013). Second, theoretical models on the evolution of animal personality based on life-history trade-offs (Wolf et al. 2007) and the pace-of-life syndrome hypothesis (Réale et al. 2010) both imply a co-variance of life-history, physiological and behavioral traits in an eco-evolutionary context (Dammhahn et al. 2018). Accordingly, adaptations of life-histories due to fisheries selection can indirectly trigger corresponding behavioral changes through correlations. Indeed, empirical evidence suggests that risky behaviors are correlated with traits indicating fast life-histories (e.g., reproductive investment; Nakayama et al. 2017), therefore, fisheries-induced adaptation of life-history could indirectly alter behavior through correlated selection. Third, vulnerability to certain fishing gear, such as hook-and-line angling or gill nets, can be strongly behaviorally dependent in certain gears (Alós et al. 2016; Härkönen et al. 2014; Klefoth et al. 2017; Rudstam et al. 1984; Sutter et al. 2012; Wilson et al. 2011; 2015). Importantly, the heritability of behavioral traits has been found to be comparable to or even higher than the heritability of life-history and morphological traits (Dochtermann et al. 2015; Mousseau and Roff 1987; Stirling et al. 2002). Thus, direct selection on behavioral traits can lead to evolution of behavioral adaptations to fishing without corresponding changes in life-history traits (Alós et al. 2016; Arlinghaus et al. 2017; Biro and Post 2008; Biro and Sampson 2015; Monk and Arlinghaus 2017; Sutter et al. 2012), in particular if there is a limited or no counter selection gradient through natural selection on behaviour.

These three mechanisms suggest that intensive and/or trait-selective fisheries can induce phenotypic and possibly genetic changes in fish personality traits; however,

there is limited theory regarding which specific behavioral changes are expected under different exploitation scenarios. Most theoretical work to date has focused on the possibility of FIE of specific personality traits, such as boldness as a proxy for risky foraging behavior in a non-novel environment (Reale et al. 2007). Specifically, a recent life-history model including boldness-related mechanisms suggested that, when fishing mortality is size-selective and exclusively directed at adults, it can be expected that evolution of a fast-life history is associated with increased shyness (Andersen et al. 2018). By contrast, exclusive harvest of juveniles was suggested to lead to the evolution of boldness when trait-selectivity is exclusively determined by size and not directly affected by behavioral traits (Andersen et al. 2018). However, the exclusive harvesting of juveniles is rare in fisheries. The model of Andersen et al. (2018) also suggests that a purely size-related, dome-shaped selectivity pattern targeting adults (typical in a harvest slot fishery) reduces or even avoids evolutionary changes in boldness. Accordingly, one can expect that positively size-selective harvesting of adults will select for shy fish, while negatively size-selective harvesting will select for bold fish. There is no corresponding theoretical work describing evolutionary changes in personality traits other than boldness (e.g., aggression, sociability, activity; Reale et al. 2007) when selection is strictly or mainly size-related, as is typical in many fisheries (Kuparinen et al. 2009).

Selection experiments can provide cause-and-effect evidence regarding FIE of both life-history and behavioral traits (Diaz Pauli and Heino 2014), but few published studies have used such an approach to focus on behavioral traits (Diaz Pauli et al. 2017; Sutter et al. 2012; Uusi-Heikkilä et al. 2015; Walsh et al. 2006). We present novel data on the evolutionary change of a range of personality traits in response to size

selection using zebrafish (*Danio rerio*) as a model system. Experimental zebrafish lines were exposed to strong directional selection pressures (a 75% per-generation harvest rate) acting on either large body size (large fishes harvested, LH) or small body size (small fishes harvested, SH). A third line was harvested randomly with respect to size (RH), serving as a control (Uusi-Heikkilä et al. 2015). Harvesting occurred over five generations, and the evolutionary outcomes in relation to life-history, physiology and behavior were examined at least three generations after the harvesting period was halted to remove ecological maternal effects and examine phenotypic changes that are most likely caused by genetic change (Uusi-Heikkilä et al. 2015). Previous results in these size-selected lines revealed substantial changes in life-history, size variation, allele frequencies and transcriptome profiles, but no change in metabolic rates (Uusi-Heikkilä et al. 2016; 2017; 2015). The SH line evolved adaptations characteristic of a slow life-history (in particular, a lower degree of reproductive investment than the control), while the LH line showed adaptations characteristic of a fast life-history (young age and small size at maturation, high relative fecundity, small terminal length). Despite the fact that these phenotypic changes seemed subtle on first glance, a model suggested they had substantial effects on population dynamics (Uusi-Heikkilä et al. 2015).

To date, behavioral changes among the zebrafish selection lines have only been examined in juveniles at F<sub>10</sub>, where, as predicted by theory (Andersen et al. 2018), SH juveniles were found to be bolder than control juveniles. In contrast, in the earlier study the LH line did not show any behavioral differences compared to the control line (Uusi-Heikkilä et al. 2015). 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), which are both important in a reproductive context (McPeck 2004; Niemelä et al. 2012). It is unclear whether the evolutionary changes in boldness reported for the juvenile stage in the SH line by Uusi-Heikkilä et al. (2015) hold for the adult life-stage.

Our objective was to examine the effects of five generations of intensive size selection, both positive and negative, on four different adult personality traits (i.e., activity, boldness, aggression, and sociability) measured at the individual-level. 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 model of Andersen et al. (2018), we predicted that positive size selection (LH line, mimicking a fishery with a minimum length limit) triggers the evolution of shy adult fishes. By contrast, we expected the evolution of bold adult fishes in the negative size selection line (SH 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 contribute to attaining a specific size on which selection operated through energy acquisition and allocation-based mechanisms (Enberg et al. 2012). Specifically, we predicted that fishes of the LH line (where small fish had a selective advantage) would be (i) more active (thereby expending more energy), (ii) less aggressive (leading to reduced access to food resources), and (iii) more social (leading to increased competition for food and reduced per capita consumption) than fishes of the control line. We expected opposing adaptations in the SH line (where large fish had a selective advantage). We also predicted that all four behavioral traits would be repeatable (i.e., indicative of

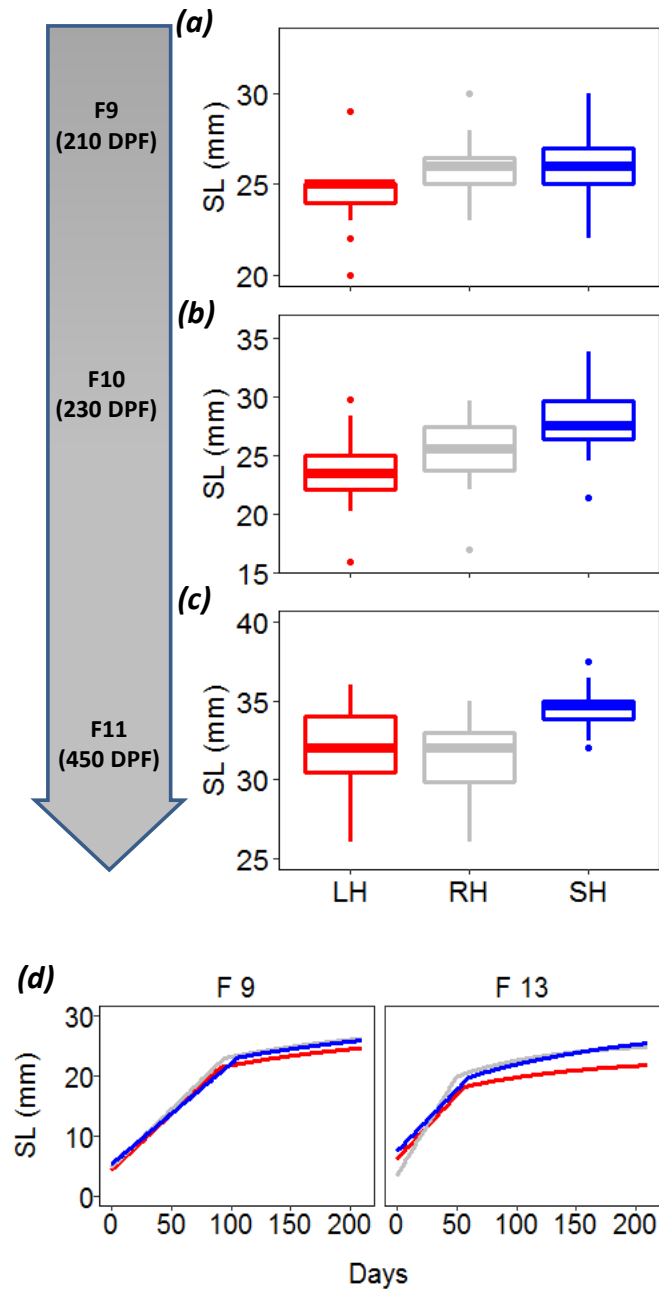


personality traits; Reale et al. 2007) and correlated amongst one another (i.e., indicative of a behavioral syndrome; Sih et al. 2004), as already demonstrated in previous studies on zebrafish (e.g., Ariyomo et al. 2013; Dahlbom et al. 2011; Moretz et al. 2007; Toms and Echevarria 2014). Given that personality is correlated with size in zebrafish (Polverino et al. 2016a), and knowing that the selection lines differ in adult body size (Uusi-Heikkilä et al. 2015; see also Fig. 1), it is possible that size differences among the selection lines could mask evolutionary adaptation in personality differences. We thus included and excluded size (body length) as a co-variate 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.

## **MATERIALS AND METHODS**

### ***Selection lines***

For our experiment, we used individuals from the F<sub>10</sub> generation of the selection lines presented in previous studies (Uusi-Heikkilä et al. 2017; 2015). Size-selective harvesting occurred during the first five generations once 50% of the randomly harvested fish were mature, after which harvesting was stopped for five generations to remove any “maternal” effects stemming from holding contexts to be able to cleanly study the evolutionary outcomes of selection as well as the maintenance of evolutionary adaptations after harvesting was stopped in common gardens (Uusi-Heikkilä et al. 2015). Zebrafish were reared in groups and maintained under the following conditions: water temperature of 26±0.5 °C; photoperiod of 12-12 h light-darkness cycle; fed ad libitum with dry food (TetraMin, Tetra).



**Figure 1.** Differences in size (standard length expressed in mm, SL) among positive (LH) and negative (SH) size-selected lines with respect to the control line (RH) that was randomly selected for size are presented across ontogeny. At F<sub>9</sub> (a; N = LH: 19; RH: 15; SH: 21) at 210 days post fertilization (DPF), F<sub>10</sub> (b; N = 100) at 230 DPF and F<sub>11</sub> (c; N = 30) at 450 DPF. Results of the Lester biphasic growth model are also presented for generations F<sub>9</sub> and F<sub>13</sub> (d). Letters above the boxplots indicate the output of the Tukey's post hoc test (a<b). More details regarding the statistical approach are presented in the supplementary material.

Comparisons among lines under common-garden conditions starting from F<sub>8</sub> onwards are then indicative of evolutionary adaptations, and corresponding genetic analysis have revealed that genetic changes have indeed taken place (Uusi-Heikkilä et al. 2015). The first life-history and life-time growth outcomes were assessed at F<sub>9</sub> and revealed that the LH line evolved a smaller adult length due to altered energy allocation patterns and greater relative fecundity (Uusi-Heikkilä et al. 2015; Fig. 1) and the SH line evolved a lower reproductive investment (Uusi-Heikkilä et al. 2015).

Evolutionary rebound of these key life-history traits from F<sub>5</sub> to F<sub>10</sub> could have happened, as indicated in other studies with silversides, *Menidia menidia* (Conover et al. 2009; Salinas et al. 2012). We therefore performed an among-generation assay of the growth trajectory of the three zebrafish selection lines examined using a Lester biphasic growth model (Lester et al. 2004) conducted at F<sub>9</sub> and F<sub>13</sub> (see the Supplementary Material for details). Our results showed that the three selection lines maintained the evolved differences in life-history and terminal length until F<sub>13</sub> (Fig. 1). Transcriptomic data also indicated that the observed differences among the LH line and controls in gene expression did not converge until F<sub>9</sub> (Uusi-Heikkilä et al. 2017). Thus, the selection lines likely maintained the evolved life-history and the underlying behavioural adaptations through F<sub>13</sub> when the present study was conducted.

Six separate selection lines (LH, RH and SH with two replicates each) were raised in separate tanks in a common recirculation system until adulthood (at about 120 days post fertilization). The conditions in the common recirculation system and in all others aquaria used in this study (see below) were the same as the rearing conditions: water temperature was maintained at  $26 \pm 0.5$  °C, photoperiod was set to a 12-12 h light-darkness cycle (light on at 07:00 am), and the fish were fed *ad libitum*

with dry food (TetraMin, Tetra) five times per day. One month before the beginning of the behavioral experiment, about 50 individual fish were randomly selected from the common recirculation system and moved to six acclimation aquaria (30x40x30 cm) and fed twice per day with dry food at 2% of tank 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, and kept in social isolation tanks (30x12x12 cm) for at least 24 hours before the experimental trials started.

### ***Experimental procedure***

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 same test environment than that where total activity was assayed), aggression and sociability. To determine the repeatability score of each behavior indicative of consistent between-individual differences in behaviors (Bell et al. 2009), the assays were repeated after 24 hours in the same order. All trials were run between 13:00 and 18:00. The fish were transferred from the individual isolation tank to the experimental arena with a dip-net. A web camera (C920 HD Pro, Logitech; <http://www.logitech.com>) was placed above the experimental arena, and a 5 min movie was recorded for each individual trial. The video recording started 60 s after the fish was placed into the experimental arena to allow for acclimation.

### ***Activity and boldness trial***

Total activity and boldness were tested in the same experimental trial in a standard open field arena (30x30 cm, 4 cm water level) in which all the walls were covered with black foil to avoid reflections. An open field test is common to study zebrafish behavior and can also be associated with exploration of a novel environment (Polverino et al. 2016a; Stewart et al. 2012). In our study, activity was defined as the total distance traveled by fish in the entire area of the arena, while 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 to risk in 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 using a mirror test, a common test to study zebrafish agonistic behavior (e.g., Gerlai et al. 2000; Pham et al. 2012). Trials were conducted in an experimental arena (30x30 cm, 4 cm of water level) in which all 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 towards its image on the mirror (Larson et al. 2006). A charge was scored when the fish suddenly accelerated towards the mirror from a distance of at least two body

lengths, as defined in previous zebrafish studies (Ariyomo and Watt 2012; Gerlai et al. 2000).

### ***Sociability trial***

Social behavior was tested in an experimental arena (68x30cm, 4 cm of water level) that was subdivided into two areas by means of a transparent plastic divider. One area (38x30 cm) was occupied by the focal fish, while the other area (30x30 cm) was occupied by a stimulus shoal, a group of 13 fish (replaced every day). The stimulus shoal was composed of randomly-selected females. All arena walls except the wall occupied by the plastic divider were covered with black plastic. Sociability in zebrafish has been previously assessed by using similar methods (Nunes et al. 2017; Pham et al. 2012). 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 towards the divider from a distance of at least two body lengths.

### ***Statistical analysis***

We used generalized linear mixed effects models (GLMM) to (i) test for differences among selection lines (LH, SH and RH) in the four behaviors (total activity, risky activity, aggression and sociability), and (ii) decompose the variance into between- and within-individual sources and estimate the repeatability scores of these four traits while controlling for significant differences in selection lines (adjusted-R). We fitted two different GLMMs using the R library MCMCglmm (Alós et al. 2017; Dingemanse and Dochtermann 2013; Hadfield 2010; Harrison et al. 2014) for each of the four behaviours. The first GLMM included selection line (as a factor with three levels: SH,

RH and LH) as a fixed effect, and the identification of the fish as a random intercept term. In this model, we used the entire dataset without considering differences in size of the fish among lines (model 1, global treatment model). The second GLMM (model 2, size-matched model) included selection line (as a factor with three levels: SH, RH and LH) and total length of the fish as fixed effects, and the identification of the fish as a random intercept term. Because selection lines and fish sizes were correlated (Fig. 1b), 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. 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, discarded the initial 20,000 iterations (burning period), and one 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 was assumed to suggest convergence (Gelman and Rubin 1992; Hadfield 2010).

Adjusted- $R$  was estimated as the quotient between the between-individual variance (the variance across random intercepts of individuals,  $V_{ind_0}$ ) and the sum of  $V_{ind_0}$  and the within-individual or residual variance (the variance associated with measurement error and phenotypic flexibility,  $V_{e_0}$ ) for a given behavioural trait, following previous studies (Dingemanse and Dochtermann 2013; Nakagawa and Schielzeth 2010). We extracted  $V_{ind_0}$  and  $V_{e_0}$  from the four fitted GLMMs and computed adjusted- $R$ s and their 95% CIs using the posterior probability distributions. To assess the significance of the adjusted- $R$  scores, a reduction in the DIC ( $\Delta$ DIC) provided by the GLMM, where

$V_{ind_0}$  was constrained to 0, was used to detect significant  $V_{ind_0}$ , with any  $\Delta DIC$  reduction larger than 2 considered to be significant. Total activity, log-transformed risky activity and sociability models were initially fit assuming a Gaussian distribution of errors. Aggression was strongly over-dispersed (excess of zeros), and a zero-inflated model was fitted instead. Zero-inflated models decompose the data into two processes: count and binomial parts of the zero-inflation. We calculated the adjusted- $R$  using the count part of each model. For the first model (global treatment model), we restricted the analysis to individuals with two observations (trials) resulting in a sample size of  $n=22$  individuals for LH,  $n=18$  for RH and  $n=22$  for SH (size range 20 – 34 mm; see Fig. S1). For the second model (size-matched model), we further restricted the individuals to those with overlapping size, resulting in a smaller sample size of  $n=15$  individuals for LH,  $n=18$  for RH and  $n=11$  for SH (size range 22 – 28 cm; see Fig. S1). Finally, we tested correlations among repeatable behaviours using Kendall's coefficient ( $r_\tau$ ) to examine for evidence of behavioural syndromes.

## RESULTS

During the 5 min experimental trials, zebrafish's total activity ranged from 1 to 29 m, while activity in the risk zone ranged from 0-11 m. Aggressive behaviour ranged from 0-84 charges. Finally, sociability ranged from 0-81 attempts to join the shoal. With the exception of aggression, all behavioural traits tested with model 1 (global treatment model without controlling for length, Fig. 2) were found to be repeatable (total activity: mean  $R = 0.32$ ; boldness: mean  $R = 0.25$ ; sociability: mean  $R = 0.47$ ; Tables 1 and 2) and all repeatable traits were interpreted as personality traits (Table 2). Thus, the aggression test we used did not result in a stable personality measure.

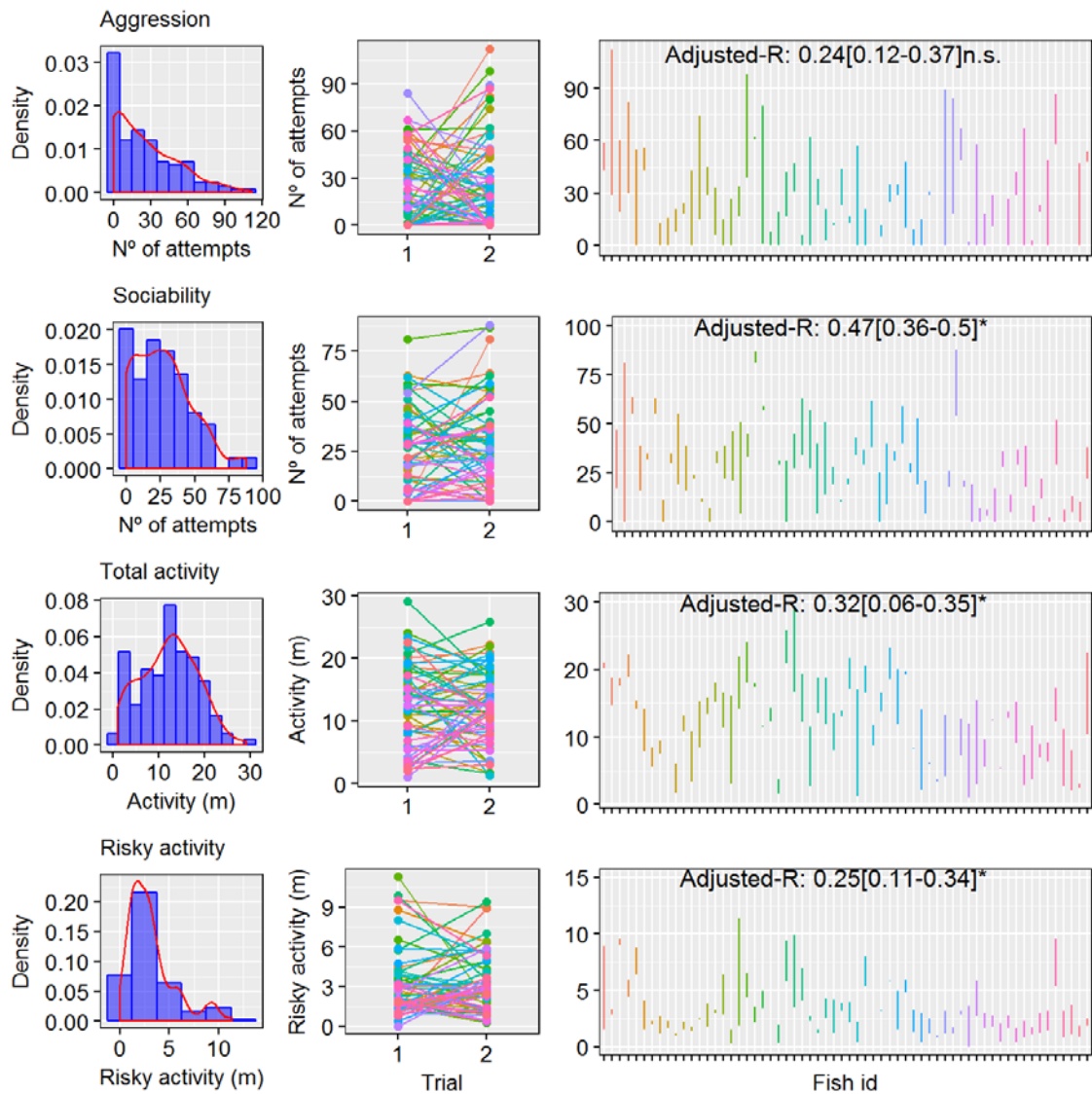


**Table 1.** Estimates of the parameters (posterior mean showed), confidential intervals (lower-CI and upper- CI) and p-MCMCs of the two generalized linear mixed models (model 1 using all individuals and model 2 using individuals with overlapping size and size as covariate) fitted for total and risky activity. Estimates for positive (LH) and negative (SH) size-selected lines are shown with respect to the control line that was randomly selected for size (RH), and fish size (cm). ID of the fish was treated as random intercept. The table also shows the deviance information criterion of the constrained model (DIC) and for the unconstrained model (DIC-un), as well as the adjusted-R scores, their confidential interval and significance of the test (\*: p value < 0.05; \*\*: p value < 0.01; \*\*\*: p value < 0.001).

Total Activity				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
(Intercept)	14733	12736	16869	<0.001***
Selection line (LH)	-435	-3048	2584	0.758
Selection line (SH)	-5750	-8747	-3148	<0.001***
DIC: 2809.1				
DIC-un: 2826.7				
Adjusted-R: 0.32[0.06-0.35]*				
Model 2				
(Intercept)	25582	1802	48999	0.032*
Selection line (LH)	-1591	-5057	2064	0.378
Selection line (SH)	-5873	-9406	-1870	0.006**
Fish size (cm)	-4243	-13228	5365	0.398
DIC: 1758.9				
DIC-un: 1781				
Log (Risky activity + 1)				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
(Intercept)	8.01	7.72	8.27	<0.001
Selection line (LH)	-0.01	-0.35	0.34	0.954
Selection line (SH)	-0.53	-0.88	-0.16	0.006**
DIC: 296.9				
DIC-un: 311.7				
Adjusted-R: 0.25[0.11-0.34]*				
Model 2				
(Intercept)	10.43	7.60	13.49	<0.001***
Selection line (LH)	-0.32	-0.79	0.12	0.160
Selection line (SH)	-0.48	-0.96	-0.01	0.044*
Fish size (cm)	-0.94	-2.18	0.13	0.120
DIC: 188.9				
DIC-un: 272.1				

**Table 2.** Estimates of the parameters (posterior mean showed), confidential intervals (lower-CI and upper- CI) and p-MCMCs of the two generalized linear mixed models (model 1 using all individuals and model 2 using individuals with overlapping size and size as covariate) fitted for sociability and aggression. Estimates for positive (LH) and negative (SH) size-selected lines are shown with respect to the control line that was randomly selected for size (RH), and fish size (cm). ID of the fish was treated as random intercept. The table also shows the deviance information criterion of the constrained model (DIC) and for the unconstrained model (DIC-un), as well as the adjusted-R scores, their confidential Interval and significance of the text (\*: p value < 0.05; \*\*: p value < 0.01; \*\*\*: p value < 0.001).

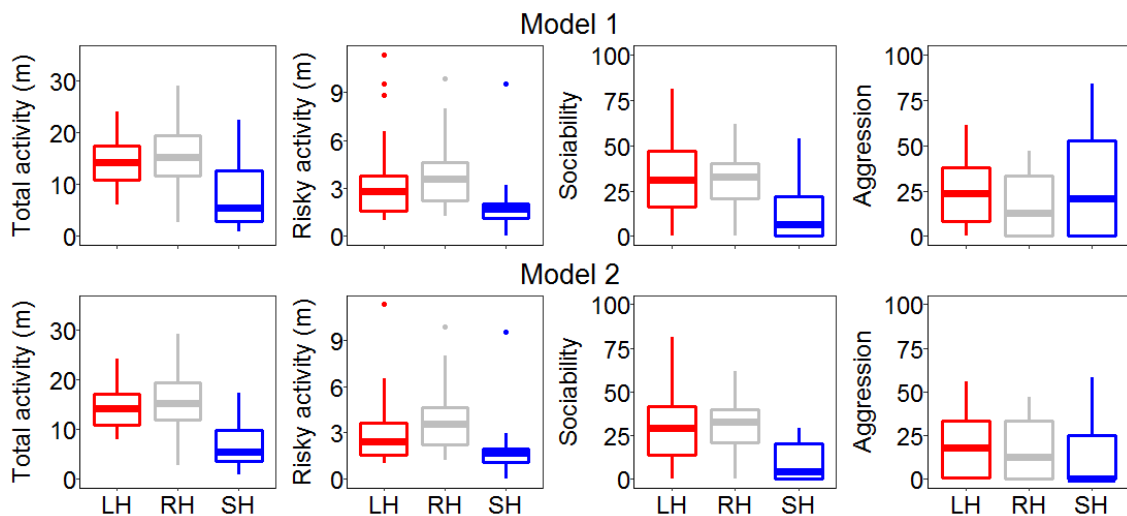
Sociability				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
(Intercept)	27.1	19.8	34.3	<0.001***
Selection line (LH)	9.2	-1.3	18.4	0.074
Selection line (SH)	-8.4	-18.0	1.6	0.116
DIC: 1328.9				
DIC-un: 1374.871				
Adjusted-R: 0.47[0.36-0.5]*				
Model 2				
(Intercept)	54.11	-20.18	128.86	0.160
Selection line (LH)	-2.58	-14.19	9.52	0.662
Selection line (SH)	-15.88	-28.54	-4.31	0.012*
Fish size (cm)	-9.13	-41.10	17.45	0.562
DIC: 741.9				
DIC-un: 769.1				
Aggression				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
(Intercept)	3.57	3.24	3.87	<0.001***
Selection line (LH)	-0.41	-0.88	-0.01	0.076
Selection line (SH)	-0.19	-0.60	0.23	0.412
DIC: 971.9				
DIC-un: 973.5				
Adjusted-R: 0.24[0.12-0.37] <sup>n.s.</sup>				
Model 2	Log ( Aggression +10)			
(Intercept)	4.42	-4.18	12.13	0.273
Selection line (LH)	0.09	-1.15	1.28	0.881
Selection line (SH)	-0.89	-2.15	0.49	0.170
Fish size (cm)	-0.77	-3.72	2.61	0.591
DIC: 522.3				
DIC-un: 522.5				
<i>Over-dispersion of the model = 0.93</i>				



**Figure 2.** Density population plots (left column), trail individual values (mid column) and among-individuals differences (right column) for each of the behaviors studied using model 1 (all individuals have been used): aggression, sociability, risky activity and total activity. The adjusted-R scores, their confidential interval and significance test for each trait are also shown.

In both models 1 (global treatment model) and 2 (size-matched model), the SH line was found to be significantly less active ( $p < 0.001$ ) and significantly less bold ( $p < 0.01$ ) compared to the control line (Table 1, Fig. 3), with no significant effect of zebrafish length (Table 1).

Additionally, while the global model did not detect a significant difference in sociability among either of the two size-selection lines relative to the control, the SH line was significantly less social than the control in the size-matched model 2 (Table 2, Fig. 3). The LH line did not differ with respect to the control in any of the behavioural traits examined (Table 2). Aggression was not compared among lines because it was not found to be repeatable (Table 2).



**Figure 3.** Differences among the selection lines in four behavioural traits (total activity, risky activity, sociability and aggression) among the positive (LH) and negative (SH) size-selected lines with respect to the control line (RH) that was randomly selected for size. Boxplots represent the mean values across the two trials for Model 1 ( $N = LH: 44; RH: 36; SH: 44$ ) and Model 2 ( $N = LH: 30; RH: 36; SH: 22$ ).

Correlation analysis among the three repeatable behavioural traits indicated that total activity and risky activity were the behavioural traits with the strongest positive correlation ( $r_{\tau}$  between 0.49 and 0.52; Table 3). Total activity was also significantly positively correlated with sociability ( $r_{\tau}$  between 0.34 and 0.39; Table 3). Risky activity and sociability were weakly, yet also significantly positively correlated ( $r_{\tau}$  between 0.21 and 0.26; Table 3), overall revealing evidence for behavioural syndromes.

**Table 3.** Correlation among repeatable behaviours (Total activity, risky activity and sociability) in each experimental trial (1 and 2) and model (global treatment and size-matched model) expressed as Kendall's coefficient. (\*: p value < 0.05; \*\*: p value < 0.01; \*\*\*: p value < 0.001).

	Total activity	Risky activity	Sociability	Total activity	Risky activity	Sociability
Model 1 – Global treatment model						
	Trial 1			Trial 2		
Total activity	-	0.50***	0.34***	-	0.52***	0.34***
Risky activity	-	-	0.21**	-	-	0.13 <sup>ns</sup>
Sociability	-	-	-	-	-	-
Model 2 – size-matched model						
	Trial 1			Trial 2		
Total activity	-	0.49***	0.39***	-	0.52***	0.37***
Risky activity	-	-	0.26*	-	-	0.23*
Sociability	-	-	-	-	-	-

## **DISCUSSION**

We found that negatively size-selective harvesting led to altered mean individual personality in female zebrafish that were tested five generations after harvesting was stopped. By contrast, and contrary to our predictions, positively size-selective harvesting did not alter any of the personality traits that we measured. Our data indicate that boldness and activity decreased in the SH line while LH did not show differences respect to controls. The differences observed in the SH line in activity and boldness did not depend on size and hence constituted a global effect of the negative size-selection treatment. We offer three alternative explanations for such results. The first relates to predation risk, the second relates to pace-of-life and the last related to social modulation of individual behaviour. Moreover, a systematic influence of size on behaviour initially masked the among-treatment sociability differences of the two size-selection lines relative to control in the global model; when controlling for size, however, individuals from the SH line were found to be significantly less sociable than control individuals. Our findings for adult zebrafish females generally agree with an earlier study on juvenile zebrafish that also found that there was no significant difference in average boldness among the LH and control lines (Uusi-Heikkilä et al. 2015).

### ***Repeatability and behavioural syndromes***

In our experimental trials, all of the behaviors except for aggression were found to be repeatable. We used experimental tests 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; Nunes et al. 2017; Pham et al. 2012). 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 behaviors that are both indicative of zebrafish boldness. Total activity and sociability also formed a syndrome, indicating that more active zebrafish are also more social. Our results agree with previous 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 a significant repeatability for this trait. Therefore, our results cannot be used to draw conclusions on aggression as a stable personality trait. Similar results have been obtained by Way et al. (2015), who compared five different behaviors of zebrafish using a mirror test and found that charges displayed by zebrafish resulted in a non-repeatable behavior. Despite the fact that charges were described as an aggressive display in other zebrafish work (Larson et al. 2006), the mirror test that we used could have been insufficient to consistently motivate individuals across trials (Way et al. 2015). Moreover, a recent study in the mangrove rivulus, *Kryptolebias marmoratus*, demonstrated that the non-reversing 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 non-reversing mirror, which could have reduced the repeatability of aggression.

### ***Boldness***

Boldness is related to the ability to acquire food resources under risk (Reale et al. 2007) and strongly contributes to mediating growth-mortality trade-offs in fishes and

other animals (Ahrens et al. 2012; Enberg et al. 2012; Stamps 2007). In this context, the evolutionary processes governing energy acquisition, allocation and growth in relation to FIE can provide putative mechanisms to explain our results, taking into account that such processes are the result of complex interactions among different selective pressures and, taken together, affect body size variation in fish (Enberg et al. 2012). Although  $F_{10}$  juveniles of the SH line were documented earlier to be bolder than controls (Uusi-Heikkilä et al. 2015), we found that, contrary to our predictions,  $F_{10}$  adult females of the SH line displayed lower levels of average boldness than females in the control line. We assumed that large size is achieved by intensive, fearless foraging, and thus the experimental removal of small fish in the SH line should have selected for bold individuals. We offer three possible explanations for the on first sight unexpected result.

In zebrafish, as in other small bodied species, larger fish are often under stronger predation risk in nature than small fish (Brown and Braithwaite 2004; Polverino et al. 2016a) because they offer more energy to gape-limited predators (Persson et al. 2003). Genotypes programmed for investing into somatic instead of gonadal growth are able to attain larger maximum size, like the individuals of the SH line (Uusi-Heikkilä et al. 2015) and thus taking less risk could be a strategy of the SH line for avoiding predation in favour of future reproduction. The fact that we found the same results after controlling for body length demonstrates that our finding is a global response to the negative size-selection and was not caused by phenotypic differences related to different body lengths among the size-selection treatments.

An alternative explanation of our findings could be related to the pace-of-life syndrome (Réale et al. 2010). Previous studies on the same selection lines documented



that the SH line maintained fast post-maturation growth at the cost of reduced reproductive investment (Fig. 1), indicative of a slow life-history (Uusi-Heikkilä et al. 2015). While the SH line was found to be bolder than the control line at the juvenile stage, we found that adult SH females were shyer than the controls. Thus, the transition at maturation appears to have reversed the personality expressed by the SH line. The pace-of-life-concept suggests that fish with slow life-history should be shy to reduce the risk of mortality in favour of future reproduction (Réale et al. 2010), which agrees with our results. Personality changes across ontogeny have also been reported in other fish species such as the Eastern mosquitofish, *Gambusia holbrooki* (Polverino et al. 2016b), while in the largemouth bass (*Micropterus salmoides*) boldness can affect fitness differently across life stages (Ballew et al. 2017). However, a clear switch has only been described in the field cricket (*Gryllus integer*), for which boldness was consistently repeatable across ontogeny 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) or altered fitness values (Ballew et al. 2017). Indeed, we found no change of boldness in adult females of the LH line, in agreement 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). However, fast life-histories (such as the life-history shown by the LH line) should be characterized by elevated boldness (Réale et al. 2010), which could have created a counterforce after

maturation leading to no change in boldness relative to the control. Our work underscores that the predictions of the pace-of-life-syndrome with respect to behavioural and life-history correlations can be context-dependent and can vary among ecological conditions, thereby complicating generalizations (Royauté et al. 2018).

The last possible explanation for the lack of evolution of shy individuals in the positively size-selected line could relate to the fact that we measured the behavior of a social fish in isolation. Isolation can create physiological stress in zebrafish (Forsatkar et al. 2017), which can lead to outcomes that do not represent what the fish 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 stickleback (*Gasterosteus aculeatus*) that showed 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 the LH line could display a different level of boldness or a different level of activity and sociability when tested in shoals. In fact, preliminary findings suggest that, when in shoals, the LH fish take less risks, and SH fish take more risks, than control fish (Sbragaglia et al. unpublished data). This suggests that one must be cautious with classical personality tests of focal individuals when the actual selection environment is in a social setting, as was the case in our harvesting experiment. Therefore, future work on this model system should focus on behavioural change in groups and across ontogeny, particularly because given that zebrafish is a

social fish the phenotypes expressed in a social environment will be the ultimate outcome of adaptation to size-selection.

Despite the possibility that our measures of total activity and risky activity could be measures of the same latent personality trait (i.e., boldness), it could be possible that total activity represents a separate trait that is correlated with boldness (Reale et al. 2007). The fact that we found lower activity in the SH 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 SH line that evolved a larger terminal size than the LH line evolved a lower average activity compared to the control line.

Our work constitutes the first empirical test of a recent theoretical life-history model of FIE of boldness (Andersen et al. 2018). That model predicts evolution of shy individuals when fishing mortality is directed exclusively at large adult fish, and evolution of bold individuals when fishing mortality also or mainly captures juveniles. Our work only partially supports the model of Andersen et al. (2018). 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 LH treatment was more adult-oriented than in the SH treatment. It is important to consider that the size-selective harvesting occurred when 50% of the control line was mature (Uusi-Heikkilä et al. 2015). All fish that survived the size-selective harvesting (either the smallest or the largest of the 25% percentile of the size distribution) 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) likely resulted in our harvesting targeting mainly (negative size-selection) or exclusively (positive size-selection) adults in both size-selection treatments, and that these effects were reinforced over generations as the maturation size and age continued to shift to smaller sizes and younger ages. Assuming that only body size determines the harvest probability (i.e., without other co-varying behavioural traits, which appears somewhat unlikely in the wild), the model of 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 only in the SH line. The unexpected result in our study was that the positive size-selection treatment (LH) did not appear to drive the evolution of increased boldness compared to the control line. However, this result for the LH adults agrees with previous findings for juveniles of the same line (Uusi-Heikkilä et al. 2015).

### ***Sociability***

The negative size-selection (SH) treatment resulted in evolutionary changes in the sociability of adult female zebrafish. We predicted that the LH and SH females would have evolved higher and lower sociability than control females, respectively. Only the latter prediction was supported by our results; the SH line evolved lower average sociability compared to the control line, while no changes were revealed in the LH line. Our hypothesis was that the SH treatment would favor low sociability because reduced social interaction would likely lead to increased consumption during the highly-competitive, clumped feedings that happened in the original harvest experiment (Uusi-

Heikkilä et al. 2015). As mentioned above, social individual-assayed personalities could result in different phenotypic outcomes at the group level (Jolles et al. 2017), and unpublished results of our research group support the notion that the SH line forms tighter shoals than the control line (Sbragaglia et al. unpublished data). This is noteworthy because shoaling behavior facilitates foraging efficiency in zebrafish (Nunes et al. 2017). Thus, less social SH individuals may have attained larger sizes during the harvesting experiment because individually asocial personality traits might lead to more cohesive groups, but this assumption necessitates a proper future test on the group differences of LH and SH fish relative to control fish. 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 appeared to be differentially affected by size and was more tightly-correlated to total activity than to risky activity, suggesting that this interpretation may be unlikely.

### ***Limitations and further study***

We provide the first experimental insights on how size-selective harvesting may trigger the evolution of fish boldness, activity and sociability in a social fish. However, our study has limitations that should be considered in future studies. First, our results were confined to females. Given that males and females can display different behaviours in zebrafish (Spence et al. 2008) our findings cannot be generalized to males. Second, in our sociability test, we used a shoaling stimulus composed of zebrafish coming 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), and thus our inferred explanation that maturation reversed personality in the SH line remains speculative. Finally, we may have overlooked important behaviours that relate to growth variation and that might also have changed together with size-selection. For example, rank in the dominance hierarchy determines food monopolization in zebrafish (Hamilton and Dill 2002). In fact, in a separate experiment with the same selection lines at  $F_{11}$  (see supplementary material), we detected a significant difference in dyadic agonistic interactions (i.e., bites) among the selection lines using size-matched males and females (Fig. S2). The results indicate that the SH 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.

## **CONCLUSIONS**

We have demonstrated that five generations of size-selection in zebrafish induced evolutionary changes in individual-level personality in females, but in unexpected ways and not consistently 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 scenarios, where the fish live in groups, have multiple spawning events, and/or with overlapping generations. Further, behavior might be under direct selection by fisheries, but our experiment strictly selected based on size. Nevertheless, at a broad level, our work suggests that exclusively size-selective

harvesting has the potential to alter personality traits five generations after harvesting was stopped. In that sense, our work supports recent theoretical work that predicts size-selected fisheries alters behaviour (Andersen 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). Further work is needed to examine how individual-level personality is expressed in a social context, particularly for social species such as zebrafish. These findings demonstrate that fish personalities could evolve in response to size selection, and that these changes can be maintained for at least five generations after the selection pressure by harvesting is stopped.

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### **Contributions**

RA, SUH and AW conceived the experiment. VS, KF, CTM and CD-G conducted the experiment and behavioral analysis. VS, JA, and AEH performed statistical analyses. VS

and RA mainly interpreted the results and wrote the manuscript, with feedback from all other authors.



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## SUPPLEMENTARY MATERIAL

### *Biphasic growth model*

We fit the “fixed  $g$ ” formulation of the Lester biphasic growth model (LM) (Honsey et al. 2017; Lester et al. 2004; Lester et al. 2014; Quince et al. 2008a; 2008b) to zebrafish growth data. For length at time  $t$  ( $l_t$ ), the growth trajectory is given by

$$(1) \quad l_t = l_0 + ht, \quad t \leq T \text{ for juveniles,}$$

$$(2) \quad l_t = l_\infty(1 - e^{-k(t-t_0)}), \quad t > T \text{ for adults,}$$

with

$$t_1 = -\frac{l_0}{h}$$

$$l_\infty = \frac{3h}{g}$$

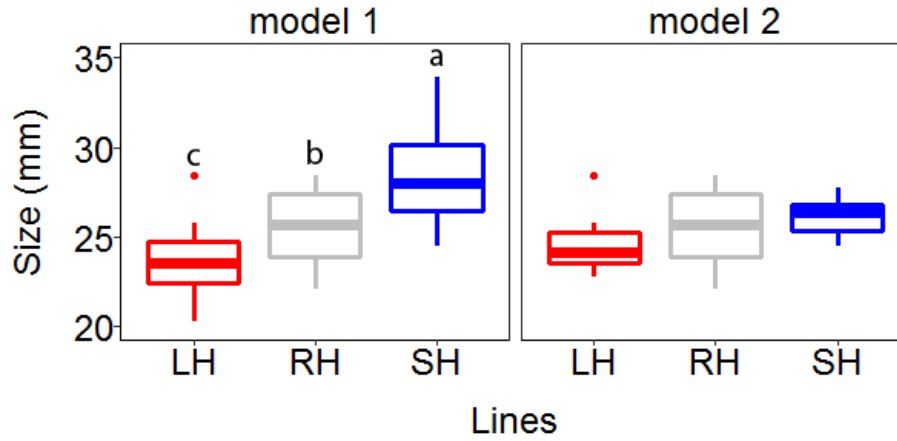
$$k = \ln\left(1 + \frac{g}{3}\right)$$

$$t_0 = T + \ln\left(1 - \frac{g(T-t_1)}{3}\right) / \ln\left(1 + \frac{g}{3}\right),$$

where  $l_0$  is the theoretical length at age 0 (mm);  $h$  is the net rate of energy acquisition expressed as juvenile somatic growth rate ( $\text{mm} \cdot \text{d}^{-1}$ );  $T$  is the last immature age, after which individuals start investing energy into reproduction (d; LM parameter for age-at-maturity);  $l_\infty$  is the asymptotic length (mm);  $k$  is the von Bertalanffy growth coefficient ( $\text{d}^{-1}$ );  $t_0$  is the von Bertalanffy theoretical age at length 0 (d);  $t_1$  is the Lester (immature) theoretical age at length 0 (d); and  $g$  is the cost to somatic growth of maturity (expressed in equivalent energetic units), which is often assumed to be dominated by energetic investment in reproduction (Honsey et al. 2017; Kozłowski 1996; Roff 2002). We assumed that fish length at age  $t$  was normally distributed around the length predicted by the model for that age,  $\hat{\mu}_t(\theta)$  (Quince et al. 2008a). In

order to allow error to scale with fish size, we defined the standard deviation of this distribution,  $\sigma_t$ , as a power function of the predicted length:  $\sigma_t = \phi \hat{\mu}_t^\psi$ , where  $\phi$  and  $\psi$  are estimated parameters (See supplement in Quince et al. 2008b).

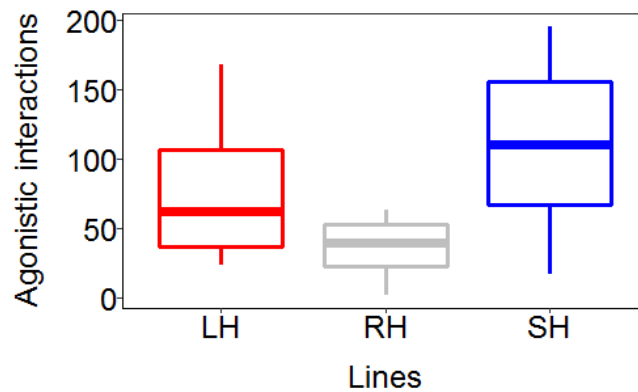
We fit the LM in a hierarchical Bayesian framework using Stan (Carpenter et al. 2017) via RStan (<http://mc-stan.org>). The hierarchical framework was constructed with selection line replicate-level LM parameters  $\theta_g$  arising as  $\theta_g \sim N(\theta_l, \sigma_\theta)$ , where  $\theta_l$  are selection line-specific parameter estimates and  $\sigma_\theta$  is the estimated standard deviation for a given line-level parameter. This framework allowed for simultaneous estimation of group- and line-level parameters and accounted for any autocorrelation within groups (similar to a random-effects model). The two variance parameters  $\phi$  and  $\psi$  were considered global, i.e., they were not estimated in the hierarchical manner described above. We fit the model to data describing each line separately. To improve model performance, we fit a linear model to the first 2-3 length-at-age data points for each line and used the slope and intercept estimates to inform priors for  $h$  and  $l_0$ , respectively, when fitting the full model. These priors were defined as  $N(\hat{\theta}, \hat{\theta}/10)$ , where  $\hat{\theta}$  are the linear model parameter estimates. This process promotes model convergence without leveraging information outside of the data and is similar to the approach used by (Honsey et al. 2017); see also (Wilson et al. 2018) Wilson *et al.*, 2018). We used vague priors for the remaining parameters. For each fit, we ran four Hamiltonian Monte Carlo (HMC) chains for 8000 iterations (3500 warmup, 4500 sampling). We used the potential scale reduction factor (Gelman and Rubin 1992) and visually examined HMC chain trace plots to assess model convergence.



**Fig. S1** – Size (Total length) of the zebrafish used for model 1 using all individuals and model 2 using individuals with overlapping sizes. Letters indicated the output of the Tukey’s post hoc test ( $a > b > c$ ) for model 1. Size was not significantly ( $F_{41,2} = 3.121$ ;  $p > 0.05$ ) different among lines in model 2. Model 1 ( $N = LH: 22$ ;  $RH: 18$ ;  $SH: 22$ ) and Model 2 ( $N = LH: 15$ ;  $RH: 18$ ;  $SH: 11$ ).

### ***Dyadic agonistic interactions***

We paired one female and one male for each selection line. The previously unfamiliar individuals were randomly taken from acclimation aquaria and housed in 5 L spawning boxes. Once in the acclimation aquaria we created size-matched populations to isolate the behavioural component of agonistic interaction. The boxes were placed in a recirculating water system and maintained at a water temperature of  $26 \pm 0.5$  °C, under a 10-14 h light darkness cycle (light on at 07:00 am) and fed with dry food (TetraMin, Tetra). Each box was separated from the others in order to allow scoring of behaviour of one box without disturbing the others. To that end, a divider was raised, and the number of bites was counted for five minutes after the first bite. Within a given box, the two individuals were kept separated by a sponge for the first 24 hours. Agonistic interactions (i.e., biting is the most common aggressive behavior in zebrafish; Paull et al. 2010) were then observed between 09:00 and 13:00. The number of bites was square-rooted transformed and modelled with a linear model. Model fitting has been assessed by checking the plot of the residuals vs. the fitted values. Results indicated that SH line displayed significantly more aggressive interaction (considering both female and male bites) than control in dyadic contest ( $F_{2,21} = 4.54$ ;  $p < 0.01$ ). Only a weak trend was observed for LH to be more aggressive than control ( $F_{2,21} = 4.54$ ;  $p = 0.10$ ).



**Figure S2.** Differences in agonistic interactions (number of bites) among positive (LH) and negative (SH) size-selected lines with respect to the control line (RH) that was randomly selected for size during dyadic contests between one male and one female at 120 days post fertilization at  $F_{11}$  ( $N = 8$ ).

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