Original Article

Size-selective harvesting impacts learning and decision-making in zebrafish, *Danio rerio*

Tamal Roy,[a,] Tabea Rohr,[b] and Robert Arlinghaus[a,c,]

[a]Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany, [b]University of Potsdam, Faculty of Science, Karl-Liebknecht-Str. 24-25, 14476 Potsdam, Germany, and [c]Division of Integrative Fisheries Management, Department of Crop and Animal Sciences, Faculty of Life Sciences, Humboldt University of Berlin, Unter den Linden 6, 10099 Berlin, Germany

Size-selective harvesting common to fisheries is known to evolutionarily alter life history and behavioral traits in exploited fish populations. Changes in these traits may, in turn, modify learning and decision-making abilities through energetic trade-offs with brain investment that can vary across development or via correlations with personality traits. We examined the hypothesis of size-selection induced alteration of learning performance in three selection lines of zebrafish (*Danio rerio*) generated through intensive harvesting for large, small and random body-size for five generations followed by no further selection for ten generations that allowed examining evolutionarily fixed outcomes. We tested associative learning ability throughout ontogeny in fish groups using a color-discrimination paradigm with a food reward, and the propensity to make group decisions in an associative task. All selection lines showed significant associative abilities that improved across ontogeny. The large-harvested line fish showed a significantly slower associative learning speed as subadults and adults than the controls. We found no evidence of memory decay as a function of size-selection. Decision-making speed did not vary across lines, but the large-harvested line made faster decisions during the probe trial. Collectively, our results show that large size-selective harvesting evolutionarily alters associative and decision-making abilities in zebrafish, which could affect resource acquisition and survival in exploited fish populations.

Key words: cognition, collective behaviordevelopment, fisheries-induced evolution, life history traitssize-selective mortality.

INTRODUCTION

Intensive harvesting can cause evolutionary changes in animal populations (Allendorf and Hard 2009; Kuparinen and Festa-Bianchet 2017; Festa-Bianchet and Mysterud 2018). A prominent example of intensive harvesting is fisheries where fish are often targeted based on their body size (Jørgensen et al. 2009; Matsumura et al. 2011; Kendall et al. 2014). While catching large-sized fish is prevalent in most commercial and recreational fisheries, some fishing gears, or fisheries governed by certain size-based regulations (e.g., maximum-size limits) may also selectively catch the smaller members of fish populations (Jørgensen et al. 2009; Kuparinen et al. 2009; Heino et al. 2015). Harvesting both large-and small sized fish generation after generation may evolutionarily alter not only the life history and morphology (Jørgensen et al. 2009; Matsumura et al. 2011; Kendall et al. 2014), but also physiological (Redpath et al. 2010; Hollins et al. 2018; Renneville et al. 2020) and behavioral traits such as boldness (Leclerc et al. 2017;

Andersen et al. 2018). Changes in life history and behavioral traits due to intensive harvesting may also result in evolutionary changes in cognitive abilities (Enberg et al. 2012). Cognition is key for acquiring resources, avoiding dangers and responding to changing environments (Shettleworth 2010), such that any fisheries-induced changes to cognitive abilities may impact survival, and in turn, population dynamics. In this study, we experimentally investigate if intensive size-selective mortality fosters evolutionary changes in collective learning and decision-making using zebrafish, *Danio rerio*, as an experimental harvest model.

One of the most consistent findings of theoretical and empirical studies on fisheries-induced evolution is that elevated and selective harvesting of large-sized fish typical of most fisheries fosters the evolution of a fast life history characterized by early maturation, increased reproductive investment, rapid juvenile (but reduced adult) growth, and reduced longevity (Rijnsdorp 1993; Hamilton et al. 2007; Jørgensen et al. 2007). Based on the pace-of-life syndrome hypothesis, animals demonstrating a fast life history are expected to also express fast behavioral phenotypes (Réale et al. 2010). This is expected to result in faster learning and enhanced memory abilities

Address correspondence to T. Roy. E-mail: bionictam@gmail.com.

to accelerate resource acquisition for early and elevated investment into reproduction. But, an increased investment in reproduction to fuel a fast life history can be expected to be traded off with decreased investment in other energy expensive tissues like the brain (Energy tradeoff hypothesis: Isler and van Schaik 2009) which in turn might lower cognitive ability of fish adapted to elevated and positive size-selective mortality. The brain is the seat of cognition and is the most energetically expensive organ in vertebrates (Raichle and Gusnard 2002). A higher metabolic expenditure for brain development is often evolutionarily traded off with lower metabolic investment in other expensive tissues (Navarrete et al. 2011; Tsuboi et al. 2015). Thus, increased investment into gonads or reproduction more generally may result in reduced brain development and this in turn would result in reduced learning, memory, and decision-making abilities (Kotrschal et al. 2015; Buechel et al. 2018; Boussard et al. 2021). Previous studies have experimentally demonstrated the metabolic conflict between brain and other energetically expensive tissues. For example, in guppies *Poecilia reticulata* selected for brain size, large-brained females outperformed small brained females in a numerical learning task but the large brain lines had smaller guts and produced fewer offspring, suggesting trade-offs with physiological and reproductive performance (Kotrschal et al. 2013). Yet, the relationship between cognition and life history is not clear because fish demonstrating fast life histories might also maintain investments into cognition while allocating energy into gonads and reproduction, and achieve this by sacrificing investment into somatic growth and tissue maintenance (Laskowski et al. 2021). Accordingly, fish with fast life histories may also have larger brains as shown in 21 species of killifish (Sowersby et al. 2021), and brain size might not correspond with improved cognition in all dimensions (Buechel et al. 2018; Fong et al. 2019). It is an open question whether and to what degree size-selective harvesting alters the cognitive ability of evolving fish populations.

Cognitive abilities of animals are also correlated with behavioral types and personality traits such as boldness (Sih and Del Giudice 2012; Dougherty and Guillette 2018). Bolder, more exploratory and active fish are often fast learners and decision makers because they have a higher probability of encountering resources compared to shyer and less active fish (Shettleworth 2010; Griffin et al. 2015). For example, in Panamanian bishop fish *Brachyraphis episcopi*, individuals that explored more were faster at learning a simple association to access food (DePasquale et al. 2014). In wild-caught zebrafish, populations that took higher risks to feed in the presence of predators (Roy et al. 2017; Roy and Bhat 2018b) were also faster in learning an associative task and had a longer-lasting memory (Roy and Bhat 2018a). Size-selective harvesting fosters evolutionary changes in boldness as demonstrated through models (Arlinghaus et al. 2017; Andersen et al. 2018; Claireaux et al. 2018) and empirical investigations (Medaka *Oryzias latipes*: Diaz Pauli et al. 2019; zebrafish: Sbragaglia et al. 2021; Roy and Arlinghaus 2022). Specifically, positive size selection characterized by the removal of large-sized individuals from fish populations tends to favor the evolution of shyness (Claireaux et al. 2018; Monk et al. 2021). Therefore, for energy allocation reasons and correlations with behavior, it is possible that the cognitive abilities of fish are evolutionarily shifted toward slower learning and reduced memory ability in response to large size-selective harvesting common to many fisheries globally.

Learning abilities typically change throughout ontogeny because of brain development with increasing age (Spear and Campbell 2014). Learning and memory abilities increase with ontogenetic age as demonstrated in several fish species (guppies: Boussard et al. 2021; striped knifejaw *Oplegnathus fasciatus*: Makino et al. 2006; jack mackerel *Trachurus japonicus*: Takahashi et al. 2010; zebrafish: Valente et al. 2012). Yet, as investment in brain development has a tradeoff with investment in reproduction (Isler and van Schaik 2009; Kotrschal et al. 2013), shifts in brain development may be associated with the onset of maturation (Buechel et al. 2019). The cognitive abilities change throughout ontogeny because of a transition from resource acquisition fueling growth at the juvenile stage to resource acquisition fueling reproduction when adult (Buechel et al. 2019; Axelrod et al. 2020). Large size-selective harvesting often favors early maturation (Hamilton et al. 2007; Kendall et al. 2014) and this may cause changes in the pace of brain development, which may reduce cognitive abilities in adults after the onset of maturation. Further, as alluded before, cognitive abilities are often correlated with animal personality (Kareklas et al. 2018; Bensky and Bell 2020), and animal personality expression is often consistent within, but not necessarily across life history stages (Groothuis and Trillmich 2011; Cabrera et al. 2021), as shown in several fish species (killifish *Kryptolebias marmoratus*: Edenbrow and Croft 2011; Eastern mosquitofish *Gambusia affinis*: Polverino et al. 2016; zebrafish: Roy and Arlinghaus 2022; Sbragaglia et al. 2022b). Hence, a change in personality over ontogeny may be associated with a change in learning ability. Size-selective harvesting caused changes in risk-taking behavior through development in experimentally harvested zebrafish lines (Roy and Arlinghaus 2022). Large size-selective harvesting resulted in shy tendencies wheLondon, UK:n tested collectively while small size-selective harvesting resulted in increased boldness in adults (Sbragaglia et al. 2021; Roy and Arlinghaus 2022), but not in < 30-day-old juveniles (Roy and Arlinghaus 2022). Whether these ontogenetic differences in harvest-induced personality expression are associated with ontogenetic changes in associative learning is a major focus of the present work.

We tested associative ability in fish groups because this has higher ecological relevance as group living offers adaptive benefits (Krause and Ruxton 2002) in a gregarious species like zebrafish (Suriyampola et al. 2016). Also, several exploited fish species, especially the pelagic ones, are group living in nature (Croft et al. 2003). We used three experimental lines of zebrafish generated by harvesting for large, small, and random body size for five generations (Uusi-Heikkila et al. 2015, 2016, 2017) followed by no selection for 10 generations during which fish were reared and maintained through random breeding. The large-harvested line resembles the scenario in global fisheries where large-sized fish are harvested. The small-harvested line resembles fisheries where maximum-size limits exist or in case of natural predation where mainly the smallest size classes are targeted by gape-limited predators. Previous work has shown that these selection lines evolved different life histories and showed genetic adaptations, indicative of evolutionary change (Uusi-Heikkila et al. 2015, 2017).

We first tested associative learning in groups through ontogeny. We predicted that the large size-selective harvesting would result in reduced associative learning ability in adults, but not in juveniles. We expected this because the large-harvested line showed shy tendencies as adults but not as juveniles (Roy and Arlinghaus 2022) and the energy allocation differences should manifest particularly strongly after maturation. Second, we examined collective decision-making in adults using an associative task (Kareklas et al. 2018; Hansen et al. 2021). Collective decisions in fish could be affected by group cohesion (a measure of shoaling behavior) and within-group variability (Jolles et al. 2017), as fish groups with higher behavioral

variability are less cohesive and reach agreement later (Ioannou and Dall 2016). As the small- and large-harvested line showed increased and decreased shoal cohesion (Sbragaglia et al. 2022a) respectively, and decreased and increased behavioral variability (Roy and Arlinghaus 2022) compared to the controls, we predicted that the small-harvested line will make faster collective decisions while the large-harvested line will make slower decisions than the control populations.

MATERIALS AND METHODS
Selection lines

We used three selection lines (large-, small-, and random-harvested) of zebrafish, each with a replicate. These lines were generated by subjecting a wild population of zebrafish to intensive (>75% per generation) size-selective harvest for five consecutive generations (Uusi-Heikkila et al. 2015). 25% of the largest and smallest individuals were used as parents in successive generations in the small- and large-harvested lines while 25% of random individuals served as parents to produce the control line. Fish were harvested every generation based on when the 50% of the control line became mature (Uusi-Heikkila et al. 2015). The selection lines were assessed for evolved differences in key life-history traits from F_{11}. The large-harvested line evolved a fast life history characterized by elevated reproductive investment, smaller terminal body size, early maturation and reduced adult growth while the small-harvested line evolved a slow life history characterized by reduced reproductive investment and no change in adult body size compared to the control line (Uusi-Heikkila et al. 2015). The selection lines also differed in broad-scale gene expression and allele frequencies showing that the phenotypic differences have genetic underpinnings and were not merely the result of phenotypic plasticity (Uusi-Heikkila et al. 2015, 2017; Sbragaglia et al. 2021). Size selection was stopped beyond F_6, which could result in evolutionary rebound of certain life-history traits as shown in other studies (Conover et al. 2009; Salinas et al. 2012). But among-generation assays of growth trajectory conducted at F_9, F_{11}, and F_{13} using Lester biphasic growth models clearly demonstrated that the selection lines maintained the evolved differences in body size and growth rate (Sbragaglia et al. 2019b; Roy et al. 2021; Sbragaglia et al. 2021, Supplementary Figure S1). Studies in F_{13} also showed differences in reproductive behavior (Sbragaglia et al. 2019b; Roy et al. 2021), physiological traits (Sbragaglia et al. 2021), and genetics (Uusi-Heikkila et al. 2017; Sbragaglia et al. 2021), and studies conducted in F_{13} and F_{16} showed differences among lines in personality traits (Sbragaglia et al. 2019a, 2021; Roy and Arlinghaus 2022). Thus, the phenotypic divergences among selection lines persisted at F_{16} showing evolutionary fixation of these traits. Here, we measured evolutionary outcomes of size-selection on learning behavior using the F_{16} fish groups that were used in measuring collective risk-taking behavior through ontogeny by Roy and Arlinghaus (2022).

We housed the F_{15} fish of the selection lines in the laboratory in six bare round tanks (diameter: 79 cm, height: 135 cm, volume: 320-liter) at a density of approximately 1300 fish per tank. The fish were maintained under the following conditions: water temperature 27 °C, 12:12h light: darkness photoperiod; and were fed twice a day with commercial flake food (TetraMin Tropical). Similar to the method adopted in previous studies (Roy et al. 2021; Sbragaglia et al. 2021), we bred the F_{15} fish in groups (four males and two females), pooled the embryos from each replicate line and stocked eight embryos per line into 30 3-liter boxes (Supplementary Figure S2) without any enrichment (Roy and Arlinghaus 2022). We used a total of 240 fish (8 fish × 30 groups; 5 groups per replicate line, 10 groups per selection treatment) for our experiments. We conducted the associative learning assays at four ontogenetic time points (juveniles- 27–38 days post fertilization or dpf, subadults- 69–80 dpf, adults- 112–123 and 153–164 dpf) based on Roy and Arlinghaus (2022), and collective decision-making assays in adults at 285–297 dpf age (Supplementary Figure S3).

Associative learning

We tested collective associative learning and memory ability in groups throughout ontogeny using a color discrimination paradigm (Spence et al. 2011; Roy et al. 2019) in a total of 240 fish. We used a plus-maze with arm dimensions 27 × 6 × 12 cm, converted it into a T-maze to test juveniles (27–38 dpf) by blocking one of the arms, and increased the length of the arms consecutively by 6 cm for testing subadults (69–80 dpf) and adults (112–123 dpf) (Figure 1). We tested juveniles, subadults, and adults (112–123 dpf) in a two-choice (purple-yellow and blue-brown) discrimination paradigm, and adults between 153-164 dpf in a four-color discrimination paradigm. The plus maze was used for testing adults at 153–164 dpf age similar to four-choice discrimination paradigms used previously for zebrafish (Roy and Bhat 2017, 2018a). Because preferences for primary colors like red and green affect learning abilities in zebrafish (Avdesh et al. 2012; Roy et al. 2019), we did not use these colors like previous studies with wild and lab-reared zebrafish (Spence et al. 2011; Roy and Bhat 2018a). We trained the fish in groups for six consecutive days and tested their memory on the 12th day (probe trial) without the reward. Removable colored doors separated the reward chambers from the rest of the maze. In the beginning, we transferred a group of eight fish into the start chamber and allowed them to acclimate for one minute (Roy et al. 2019). After this, we released them from the start chamber, and the fish explored the arena for 10 min. We rewarded the fish with food after the first individual entered the correct door. We recorded the trials using an overhead webcam (Logitech B910). After the experiment, we allowed the fish to swim out of the chambers and gently guided them back to the start chamber. We changed the position of the doors randomly during consecutive trials to avoid side bias. From the video recordings, we scored the time taken by a random individual to enter the correct door and start feeding. This measure of latency is based on previous studies in zebrafish (Spence et al. 2011; Roy and Bhat 2017, 2018a; Daniel and Bhat 2020) and other species (*Brachyraphis episcopi*: Brown and Braithwaite 2005; three-spined sticklebacks *Gasterosteus aculeatus*: Brydges et al. 2008; guppies: Kniel et al. 2020) that used latency to estimate learning. We also scored the number of incorrect choices (mistakes) made by all fish before any individual made a correct choice, based on previous studies in zebrafish (Kareklas et al. 2018; Roy and Bhat 2018a). We confirmed learning only if we found both the performance time and number of mistakes made by fish to decrease over successive trials, following previous studies (Roy and Bhat 2017, 2018a).

Collective decision making

We tested collective decision-making among adult zebrafish groups (McAroe et al. 2017; Kareklas et al. 2018) to enter a rewarded (red) door following the same protocol and setup (Figure 1) as the associative learning assay and using the same fish groups ($N = 30$). We transferred a group of fish into the start chamber and added
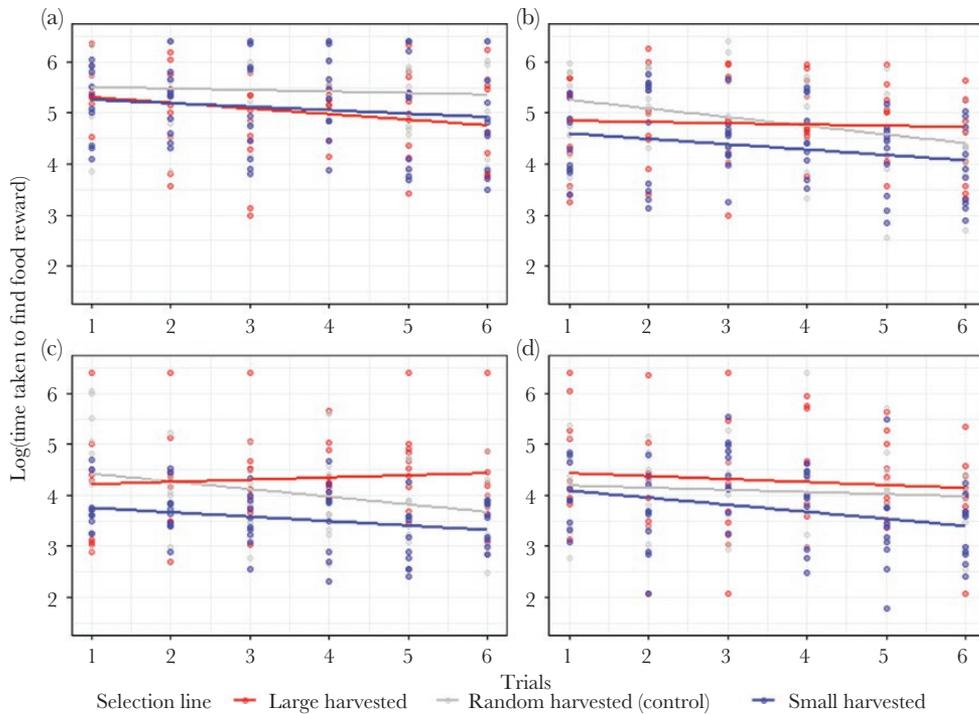
Figure 1

Plus-maze used in associative learning and collective decision-making assays. The maze was converted to a T-maze by blocking off the top arm.

food to the reward chamber during their acclimation. We released the fish and recorded their behavior for 5 min. We guided the fish back to the start chamber after the trial and changed the position of the red door. We trained fish for six consecutive days, and tested for memory on the 13th day without food reward. From the video recordings, we scored the time taken by all fish to enter the rewarded door and commence feeding as the collective decision time (Kareklas et al. 2018; Hansen et al. 2021).

Statistical analysis

We ran linear mixed-effects regression models (lmer) to examine changes in associative learning ability throughout ontogeny among selection lines. To test for changes in performance across successive trials during training at different ontogenetic stages, we first log transformed the response variable (time to find the food reward) and confirmed the normality and homogeneity of residuals. We then fitted mixed effects models using the transformed measure as the dependent variable, interaction of "Selection line," "Age" (ontogenetic stage), and "Trial" as the fixed effect and "Group ID" nested within "Replicate" as the random effect (formula: logPerformanceTime ~ Selection Line × Trial × Age + (1 | Replicate/Group ID). To test for change in the number of mistakes made across successive trials over ontogeny, we fitted a generalized linear mixed-effects model (glmer) with a Poisson structure using "Mistakes" as dependent variable, interaction of "Selection line," "Age," and "Trial" as the fixed effect and "Group ID" nested within "Replicate" as the random effect (formula: Mistakes ~ Selection Line × Trial × Stage + (1 | Replicate/Group ID). To test for the memory of fish in the selection lines, we compared the time to find the food reward on the 6th day (last day of training) and 12th day (probe trial) using paired t-test, and the number of mistakes made on the 6th and 12th day trials using a Wilcoxon paired-sample test.

We compared collective decision-making time among selection lines using lmer models. We log transformed "collective decision

time" and used this as dependent variable, interaction of "Selection line" and "Trial" as the fixed effect and "Group ID" nested within "Replicate" as the random effect (formula: logDecisionTime ~ Selection Line × Trial + (1 | Replicate/Group ID). To test for collective memory, a similar mixed model was construed and compared decision-making time on 6th and 13th day trials.

All analyses were done in R studio version 3.6.1 (R Development Core Team 2019). Logit transformation was conducted using the "*car*" (Fox et al. 2007) package, and "lmer" and "glmer" models were constructed using *lmerTest* (Kuznetsova et al. 2017) and *lme4* (Bates et al. 2012) packages. Line and box-whisker plots were made using *ggplot2* (Wickham 2011), *plyr (Wickham 2020)*, and *ggpubr* (Kassambara and Kassambara 2020) packages in R.

RESULTS

We found significant differences in performance in the associative task across selection lines over ontogeny. Specifically, the time taken to find the food reward changed significantly across trials ($F_{1,669}$ = 23, $P < 0.01$) during training, and over ontogenetic age ($F_{3,669}$ = 20.95, $P < 0.01$) for all selection lines (Figure 2). Fish took significantly less time as adults at 112–123 dpf (Stage C; $t = -3.1$, $P < 0.01$) and 154–164 dpf (Stage D; $t = -4.19$, $P < 0.01$) age compared to juveniles at 27–38 dpf age (Table 1). Mistakes made by fish decreased significantly with training ($z = -5.48$, $P < 0.01$), and adults made significantly less mistakes at 112–123 dpf (Trial × Stage C; $z = -6.92$, $P < 0.01$) but more mistakes at 154–164 dpf (Trial × Stage D; $z = 4.98$, $P < 0.01$) across trials compared to juveniles (Table 2, Figure 3).

The change in time taken to find the food reward across successive trials was significantly slower in subadults (69–80 dpf) of the large-harvested line fish (LH × Trial × Stage B; $t = 1.99$, $P < 0.05$) compared to the control line (Table 1), as indicated by a nearly flat slope (Figure 2b). Though the large-harvested line fish took less time to locate the food reward initially, the final performance time was not different than the initial, and the fish performed poorly compared to the control line fish (Figure 2b). Similarly, in adults (112–123 dpf), the change in time taken by the large-harvested line fish to find the food reward across successive trials was significantly slower (LH × Trial × Stage C; $t = 2.42$, $P = 0.01$) compared to the control line (Table 1, Figure 2c). The large-harvested line adults took less time to locate the food reward initially but this increased across trials and the final performance was significantly worse compared to the controls, as is evident from the positive slope of the regression line (Figure 2c). The rate of change in time taken to find the food reward by the small-harvested line fish did not differ significantly from the controls at any ontogenetic time-point (Table 1, Figure 2), though the elevation of the regression line fitted across performance time was always lower than the control (Figure 2b-d).

The change in number of mistakes made across trials was significantly slower in subadults (69–80 dpf) of the large-harvested line (LH × Trial × Stage B; $z = 2.20$, $P = 0.03$) compared to the controls (Table 2, Figure 3b). The same was found in adults (112–123 dpf) of the large-harvested line (LH × Trial × Stage C; $z = 9.23$, $P < 0.01$; Table 2, Figure 3c). Though the large-harvested line adults made less mistakes initially while locating the food reward, the number of mistakes increased across trials and were higher during the last trial compared to the controls, as evident from the positive slope of the regression line (Figure 3c). In adults of the small-harvested line at 112–123 dpf age, the change in number of mistakes made across trials was significantly slower compared

Figure 2

Comparison of regression lines fitted on log(time taken to find food reward) across consecutive trials during training as (a) juveniles (27–38 dpf), (b) subadults (69–80 dpf) and adults at (c) 112–123 dpf, and (d) 153–164 dpf.

Table 1

Results of lmer model comparing performance time of LH (large-harvested) and SH (small-harvested) lines with the RH (random-harvested or control line) across trials and across ontogenetic stages A (juvenile) to D (adult)

Fixed effects	Estimate	SE	df	t-value	Pr(>|t|)
Intercept	5.53	0.31	11.14	17.89	**< 0.01**
Selection line: LH	−0.12	0.44	11.14	−0.27	0.79
Selection line: SH	−0.21	0.44	11.14	−0.48	0.64
Trial	−0.03	0.06	669.00	−0.52	0.60
Stage B (69–80 dpf)	−0.11	0.31	669.00	−0.35	0.73
Stage C (112–123 dpf)	−0.96	0.31	669.00	−3.10	**< 0.01**
Stage D (153–164 dpf)	−1.30	0.31	669.00	−4.19	**< 0.01**
LH × Trial	−0.08	0.08	669.00	−1.01	0.31
SH × Trial	−0.04	0.08	669.00	−0.48	0.63
LH × Stage B	−0.44	0.44	669.00	−1.00	0.32
SH × Stage B	−0.51	0.44	669.00	−1.17	0.24
LH × Stage C	−0.28	0.44	669.00	−0.64	0.52
SH × Stage C	−0.52	0.44	669.00	−1.19	0.23
LH × Stage D	0.38	0.44	669.00	0.86	0.39
SH × Stage D	0.21	0.44	669.00	0.47	0.63
Trial × Stage B	−0.14	0.08	669.00	−1.75	0.08+
Trial × Stage C	−0.12	0.08	669.00	−1.51	0.13
Trial × Stage D	−0.01	0.08	669.00	−0.16	0.87
LH × Trial × Stage B	0.22	0.11	669.00	1.99	**< 0.05**
SH × Trial × Stage B	0.10	0.11	669.00	0.91	0.36
LH × Trial × Stage C	0.27	0.11	669.00	2.42	**0.02**
SH × Trial × Stage C	0.10	0.11	669.00	0.90	0.37
LH × Trial × Stage D	0.06	0.11	669.00	0.57	0.57
SH × Trial × Stage D	−0.06	0.11	669.00	−0.51	0.61

Significant results are in bold (marginal: "+").

to the control (SH × Trial × Stage C; z = 2.32, P = 0.02), and the number of errors were higher during the last trial compared to the control line (Table 2, Figure 3c). As adults at 154–164 dpf age, the change in number of mistakes made by the small-harvested line fish was significantly faster (SH × Trial × Stage D; z = −3.75, P < 0.01) than the control line (Table 2, Figure 3d).

Table 2

Results of glmer model comparing the number of mistakes made by large- and small-harvested lines with the random-harvested or control line across trials and across stages A (juvenile) to D (adult)

Fixed effects	Estimate	SE	z-value	Pr(>|t|)
Intercept	1.97	0.17	11.70	**< 0.01**
Selection line: LH	−0.20	0.25	−0.80	0.42
Selection line: SH	−1.23	0.28	−4.33	**< 0.01**
Trial	−0.23	0.04	−5.48	**< 0.01**
Stage B (69–80 dpf)	0.71	0.17	4.17	**< 0.01**
Stage C (112–123 dpf)	1.05	0.20	5.27	**< 0.01**
Stage D (153–164 dpf)	−0.70	0.20	−3.48	**< 0.01**
LH × Trial	−0.07	0.07	−1.10	0.27
SH × Trial	0.19	0.07	2.84	**<0.01**
LH × Stage B	−0.14	0.25	−0.56	0.57
SH × Stage B	0.57	0.29	1.97	**0.05**
LH × Stage C	−2.68	0.34	−7.91	**< 0.01**
SH × Stage C	0.24	0.32	0.73	0.46
LH × Stage D	0.25	0.31	0.83	0.41
SH × Stage D	1.90	0.31	6.08	**< 0.01**
Trial × Stage B	−0.03	0.05	−0.60	0.55
Trial × Stage C	−0.56	0.08	−6.92	**< 0.01**
Trial × Stage D	0.28	0.05	5.00	**< 0.01**
LH × Trial × Stage B	0.17	0.08	2.20	**0.03**
SH × Trial × Stage B	−0.01	0.08	−0.11	0.91
LH × Trial × Stage C	1.01	0.11	9.23	**<0.01**
SH × Trial × Stage C	0.25	0.11	2.32	**0.02**
LH × Trial × Stage D	−0.13	0.09	−1.42	0.15
SH × Trial × Stage D	−0.32	0.08	−3.75	**< 0.01**

Significant results are in bold.
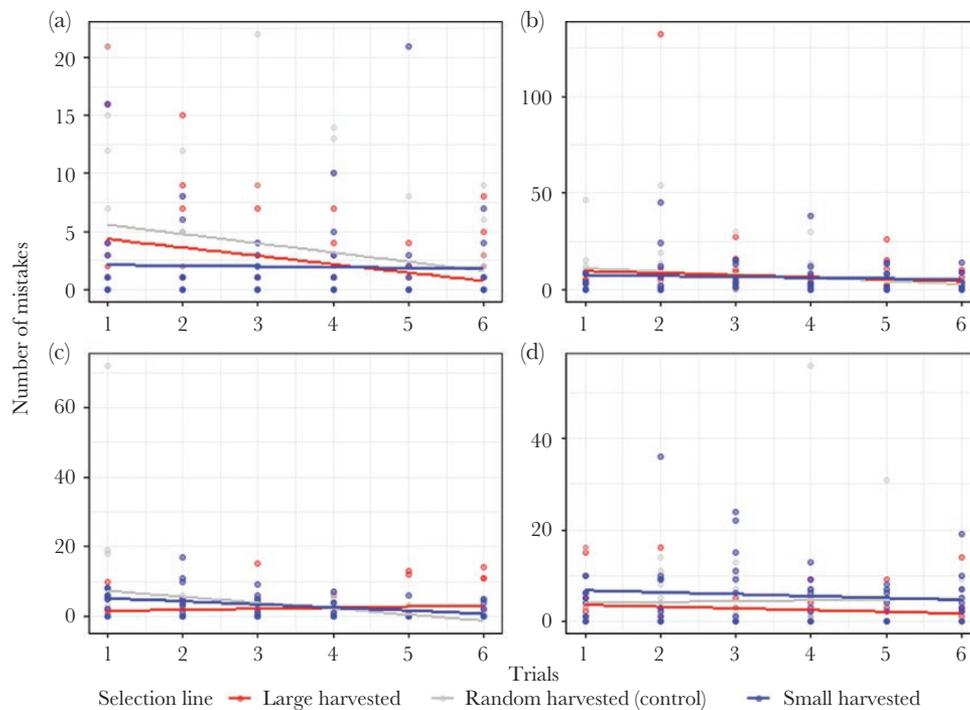
Figure 3

Comparison of regression lines fitted on number of mistakes made across consecutive trials during training as (a) juveniles (27–38 dpf), (b) subadults (69–80 dpf) and adults at (c) 112–123 dpf, and (d) 153–164 dpf.

The above-mentioned results from the training phase of the large-harvested line meant that as subadults, the fish showed slower associative performance while as adults, the fish showed significantly weaker associative abilities than the control line fish (Figures 2 and 3). To test if the performance in a maze could be explained by boldness in fish groups, we calculated

correlations between the slope of change in performance time across trials and boldness measured using the same fish groups in a previous study (Roy and Arlinghaus 2022). We did not find a significant correlation between the slopes of performance time and log(boldness measure) for any of the selection lines (large-harvested: $r < 0.01$, $P = 0.98$; random-harvested: $r = -0.01$, $P = 0.94$; small-harvested: $r = -0.04$, $P = 0.82$; Supplementary Figure S4A). We similarly estimated correlations between the slope of change in number of mistakes and boldness and did not find a significant correlation for any of the selection lines (large-harvested: $r = -0.15$, $P = 0.36$; random-harvested: $r < -0.01$, $P = 0.99$; small-harvested: $r = 0.25$, $P = 0.12$; Supplementary Figure S4B). Thus, the observed differences in performance in an associative task, especially in the large-harvested line, could not be explained by the variation in collective boldness. In tests for memory, we found no significant differences in time to find the food reward (Table 3a, Figure 4) and number of mistakes made (Table 3b, Figure 5) between the 6th and probe (12th day) trials, indicating similar retention of memory in all selection lines (Table 3a, b,, Figures 4 and 5).

In the tests for collective decision making, zebrafish generally made significantly faster decisions to enter the reward chamber over successive trials ($F_{1,147} = 26.35$, $P < 0.01$; Figure 6a). The selection lines did not significantly differ in decision-making time across trials (Selection line × Trial; $F_{2,147} = 0.94$, $P = 0.39$). Yet, during the probe (13th day) trial, we found that the large-harvested line fish took significantly less time to make decisions by entering the correct door almost immediately after their release ($t = -3.96$, P

< 0.01; Figure 6b), and the small-harvested line fish made marginally non-significantly faster decisions ($t = -1.96$, $P = 0.06$; Figure 6b), compared to the sixth trial.

DISCUSSION

Size-selective harvesting can have evolutionary consequences for adaptive personality traits (Andersen et al. 2018; Sbragaglia et al. 2021; Roy and Arlinghaus 2022). Here, we provide evidence that size-selective harvesting can also evolutionarily alter associative and collective decision-making abilities in fish. We show that performances of fish across selection lines improved significantly with ontogenetic age independent of size selection. Supporting our expectations, large size-selective harvesting resulted in slower associative abilities in subadults and adults, but these fish made speedy and accurate collective decisions when tested for memory. The slow associative abilities of the large-harvested line fish can have an impact on resource acquisition, but the improved collective decision-making ability might help them cope with certain threats. Collectively, our results provided mixed support that large size selection reduced cognitive performance, but were unable to document this effect consistently across the tests we employed. It is a common finding of cognitive research that the performance of fishes and other animals strongly varies with the cognitive task (van Horik and Madden 2016; Guenther and Brust 2017; Wallace et al. 2020).

We found that associative abilities (indicated by a decrease in the time to find a food reward and the number of mistakes) increased

Table 3

Evaluating memory performance

(a) Paired *t*-test results comparing performance time of fish during 6th- and 12th-day trials among selection lines at four ontogenetic stages A (27–38 dpf), B (69–80 dpf), C (112–123 dpf), and D (153–164 dpf). Significant results are in bold (marginal: "+").

Ontogenetic stage	Selection line	*t*	df	*P*-value
Stage A	Large-harvested	2.10	9	0.06+
	Random-harvested (Control)	3.08	9	**0.01**
	Small-harvested	1.61	9	0.14
Stage B	Large-harvested	1.29	9	0.23
	Random-harvested (Control)	0.56	9	0.59
	Small-harvested	1.47	9	0.17
Stage C	Large-harvested	1.45	9	0.18
	Random-harvested (Control)	0.54	9	0.60
	Small-harvested	5.40	9	**<0.01**
Stage D	Large-harvested	0.42	9	0.68
	Random-harvested (Control)	2.50	9	**0.03**
	Small-harvested	0.91	9	0.39

(b) Wilcoxon paired-sample test results comparing the mistakes made during 6th- and 12th-day trials among selection lines at stages A to D. Marginally significant results are indicated with "+".

Ontogenetic stage	Selection line	V	*P*-value
Stage A	Large-harvested	15	0.06+
	Random-harvested (Control)	20	0.83
	Small-harvested	6	0.79
Stage B	Large-harvested	16.5	0.51
	Random-harvested (Control)	16	0.47
	Small-harvested	18.5	0.68
Stage C	Large-harvested	17	0.21
	Random-harvested (Control)	3	0.07+
	Small-harvested	10	1
Stage D	Large-harvested	25	0.84
	Random-harvested (Control)	15	0.73
	Small-harvested	14	0.62
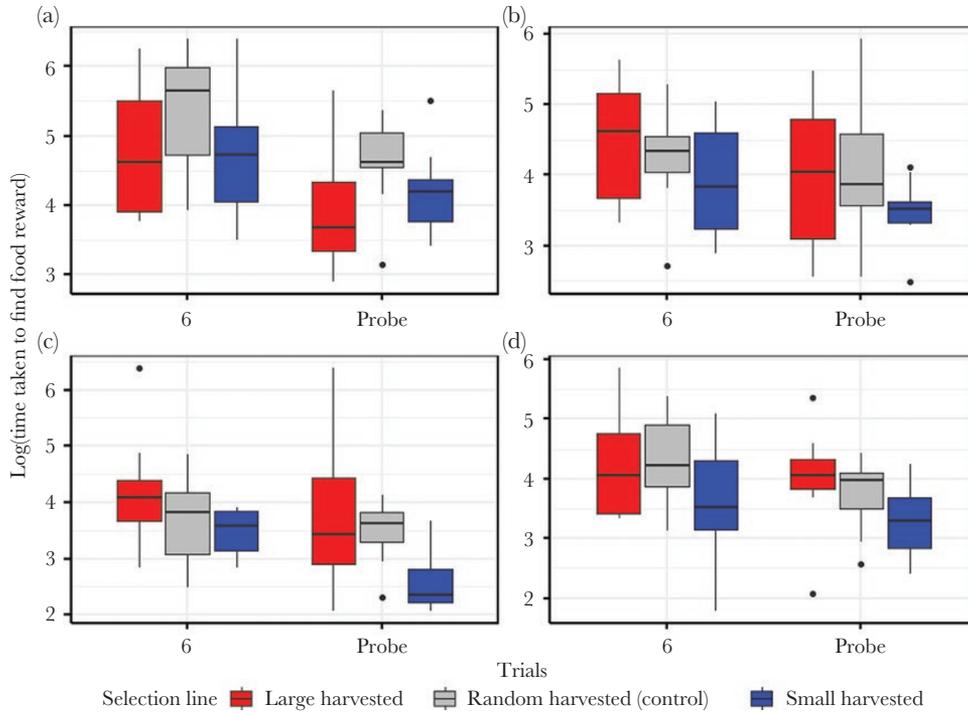
Figure 4

Comparison of log(time taken to find food reward) across selection lines on 6th- and 12th-day (probe) trials as (a) juveniles (27–38 dpf), (b) subadults (69–80 dpf) and adults at (c) 112–123 dpf, and (d) 153–164 dpf.
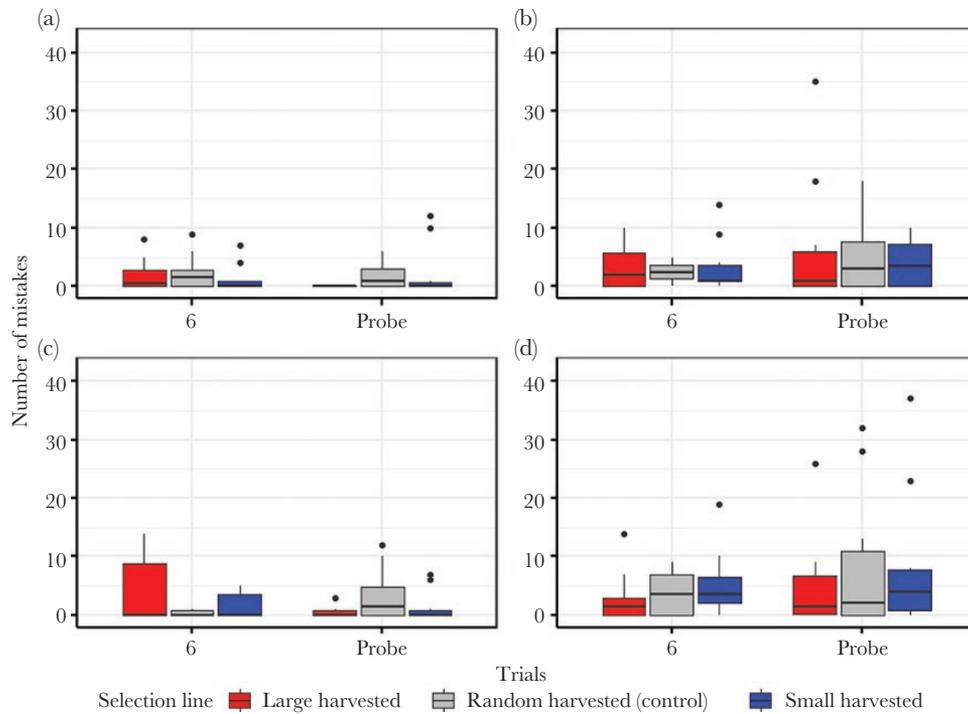

Figure 5

Comparison of mistakes made on 6th- and 12th-day (probe) trials as (a) juveniles (27–38 dpf), (b) subadults (69–80 dpf) and adults at (c) 112–123 dpf, and (d) 153–164 dpf.

throughout ontogeny in all selection lines, as would be predicted (Spear and Campbell 2014). Older fish were significantly faster in locating the food reward even though we increased the size and/or

complexity of the maze size at every ontogenetic time point. This could be due to two reasons. With the development of brain, fish are typically quicker in learning the location of the food reward
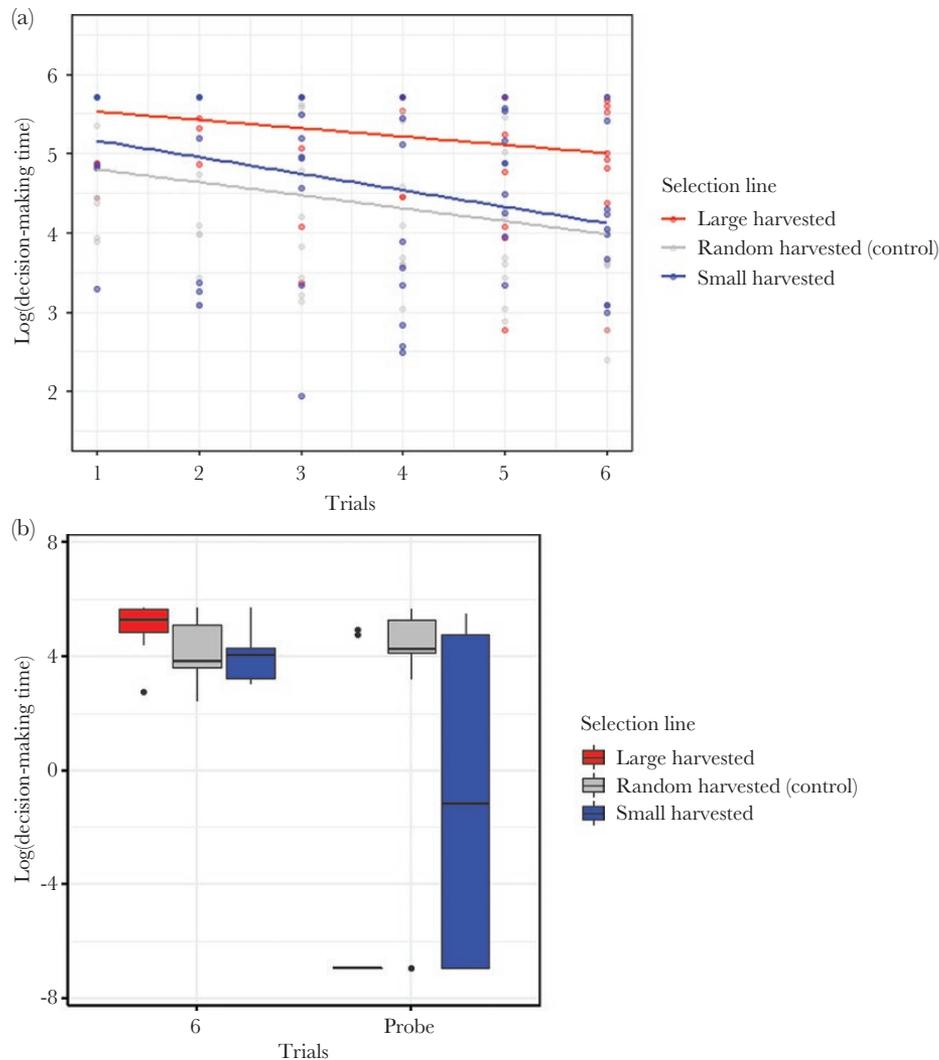
Figure 6

Comparison of (a) regression lines fitted on log(decision-making time) across trials, and (b) decision-making time during 6th- and 13th-day trials.

(Spear and Campbell 2014). Alternately, swimming speeds of fish increase with ontogenetic age (Muller et al. 2000; Müller 2020), and fish could have reached the rewarded door faster as they grew in size. But, this can only be a part of the explanation because the fish also made fewer mistakes across trials as adults, indicating better learning.

We also found that the large-harvested line fish showed slower associative abilities as subadults and adults in a simple color-discrimination task. This finding agreed with our expectation that the large-harvested fish that exhibit a fast life history and shy behavior would be slower in learning associations due to possibly lower brain investment and shy behavioral tendencies. Our results are consistent with the energy-tradeoff hypothesis (Isler and Van Schaik 2006, 2009). Increased reproductive investment may be traded-off with decreased investment in expensive body tissues like brain (Isler and Van Schaik 2006, 2009). In zebrafish, as in other species, large size-selective harvesting fosters the evolution of a fast life history characterized by increased reproductive investment (Arlinghaus et al. 2009; Uusi-Heikkila et al. 2015; Renneville et al. 2020) and this might lead to decreased energetic investment for the development of neuronal tissues in brain. Reduced brain investment may

result in decreased learning abilities (Kotrschal et al. 2013, 2015). However, the link between brain investment and learning ability among the selection lines remains speculative and the quantification of energy allocation pathways is necessary. The fact that the large-harvested zebrafish are also shyer (Sbragaglia et al. 2021; Roy and Arlinghaus 2022) reinforced the slower associative abilities, similar to other studies that revealed that shy fish show reduced associative learning abilities (Trompf and Brown 2014; Kareklas et al. 2017).

We did not find significant relationships between collective boldness (Sbragaglia et al. 2021; Roy and Arlinghaus 2022) and associative performance within the large-harvested line (and the other two lines). Thus, collective personality of the fish groups could not explain their associative abilities in the maze. Therefore, our findings imply that evolution of a fast life history in the large-harvested line fish promoted reduced group ability to solve an associative task and this could negatively affect resource acquisition by reducing the potential to locate and harvest resources (Laskowski et al. 2021). In the small-harvested line, the differences in change in error rate between the two adult stages (Figure 3c, d) could be because in the latter stage, we used a four-color discrimination paradigm to

test associative learning. The relatively higher mistakes during initial trials followed by a decline could be because there were more chambers to explore.

We exclude the possibility that our results on the observed differences among the selection lines in the associative task was confounded by behavioral variability and group cohesiveness, metabolism or swimming performances. In previous work, the large-harvested line fish showed higher behavioral variability as subadults and adults (Roy and Arlinghaus 2022), and these fish formed less cohesive shoals than the control line fish (Sbragaglia et al. 2022a, 2022b) but their shoal cohesion did not change across ontogeny (Sbragaglia et al. 2022b). In our study, the large-harvested line made fewer number of mistakes in the initial trials compared to the control line fish (Figure 3b, c) suggesting more group cohesion. The errors made increased with training in adults suggesting that as the maze became familiar, the fish explored more. In tests for swim speed, the large-harvested line fish did not differ in swimming speed from the control line fish (Sbragaglia et al. 2022a) but in our study, the large-harvested line differed significantly in the time taken to find the food reward than the controls. Thus, swim speed could not be the reason for the observed differences. Uusi-Heikkila et al. (2015) also measured standard metabolic rates among the selection lines but did not find any significant difference. Therefore, the metabolic rates of fish are unlikely to have affected their behavior in maze. We also controlled the hunger levels in fish by starving them before the tests and never feeding them in their holding tanks and so this could also not have affected the observed differences in the associative task. Here, we did not measure the body-size of fish across ontogeny but the fish likely differed in size-at-age (Uusi-Heikkila et al. 2015, 2016). Our results across lines could have been confounded by body-size differences and this effect cannot be separated.

We found that the fish across all selection lines made quicker decisions to enter the reward chamber over successive trials. This is similar to a previous study in guppies where groups of fish made faster collective decisions to avoid a predator (Hansen et al. 2021). Improvement in decision-making speed over trials could be due to social facilitation (Brown and Laland 2003) where one or more individuals enable others to find the food reward and the facilitation process speeds up over successive trials. The fish could also get more habituated with the setup over successive trials resulting in a decrease in decision-making time. The large-harvested line fish collectively entered the reward chamber significantly faster and almost instantaneously post-release during the probe trial compared to the sixth-day trial. This does not agree with our expectation that the large-harvested line will make slower decisions because they are less cohesive and individually more vigilant (Sbragaglia et al. 2022a), and demonstrate higher within-group behavioral variability (Roy and Arlinghaus 2022). However, Sbragaglia et al. (2021) and Roy and Arlinghaus (2022) also showed that the large-harvested line fish demonstrated shy behavioral tendencies as adults. After the six-day interval period, the low risk-taking tendency could have driven all fish to choose the red door compartment together. Red is a preferred and attractive color for zebrafish (Avdesh et al. 2012; Roy et al. 2019) and all individuals chose to enter this preferred door leading to an instantaneous decision that may be an outcome of shyness.

Though we saw differences in associative and decision-making abilities among selection lines, the fact that selection was stopped for 10 generations might have caused some trait recovery after the initial bout of selection and evolution. Studies in Atlantic silverside *Menidia menidia* have shown that stopping selection for a couple of generations after size-selective harvesting induced evolutionary changes in life-history traits led to partial trait recovery (Conover et al. 2009; Salinas et al. 2012). Yet, the feeding rate in silversides did not bounce back to pre-harvesting levels after selection was stopped, which indicated that this trait was evolutionary fixed (Salinas et al. 2012). As our study tested learning and decision-making while finding food, the studies in silversides lend some support by showing that stopping selection might not have hampered the feeding behavior of size-selected fish. The differences observed among selection lines in our study could be further due to factors like density (Bouffet-Halle et al. 2021; Crespel et al. 2021a, 2021b) and genetic drift (Therkildsen et al. 2019). A recent study in medaka showed that life-history divergence may not be caused by direct harvest selection but by density-dependent selection for a larger body size (Bouffet-Halle et al. 2021). Though we held fish at a uniform density of eight individuals per box right from the embryonic stage and throughout the period of experiments, there might have been differences in density in the holding tanks during rearing and development. These differences in population developmental density can determine the evolutionary potential of size selection (Crespel et al. 2021a). Genetic drift may cause differences between the selection line replicates as shown in Atlantic silversides (Therkildsen et al. 2019) and this may account for the variations among selection lines. Another limitation of this study is the non-existence of an unharvested control which may better represent a wild or unexploited population.

CONCLUSIONS

Our work extends the evolutionary consequences of harvesting from the much-studied life history and behavioral domains to the cognitive domain. Size-selective harvesting typical of most commercial and recreational fisheries had the most significant impact on associative learning and group decision-making in zebrafish by reducing learning speed but strengthening collective decision memory. These effects could affect growth and survival of exploited populations because learning and making timely decisions are crucial for finding resources, avoiding dangers and adapting to changing environments. Further investigations are warranted to understand if the observed differences across selection lines extend to other cognitive abilities, whether reduced learning is due to reduced brain size and reduced neuronal cell count and density as a tradeoff with reproduction as supposed (Isler and van Schaik 2009; Kotrschal et al. 2013; Marhounová et al. 2019), and whether altered cognitive abilities affect survival against natural and human predation. One possible outcome could be an increased natural but decreased gear-induced mortality associated with reduced collective associative performance in fish evolutionarily adapted to large size-selection, as predicted by a previous modeling study by Sbragaglia et al. (2022a). But, whether this actually happens has to be examined through detailed experiments that would test the propensity of the selection lines to get caught in active and passive gears, and to be predated upon by fish predators.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

AUTHOR CONTRIBUTIONS

T.R. and R.A. conceived the study. T.R. performed the associative learning assays and Ta.R. conducted the collective decision-making experiment. T.R. analyzed and interpreted the data and wrote the manuscript with inputs from R.A.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Roy et al. (2023).

Handling Editor: Emilie Snell-Rood

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