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Size-selective harvesting fosters adaptations in mating behavior and reproductive allocation, affecting sexual selection in fish

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ABSTRACT

1. The role of sexual selection in the context of harvest-induced evolution is poorly understood. However, elevated and trait-selective harvesting of wild populations may change sexually-selected traits, which in turn can affect mate choice and reproduction.
2. We experimentally evaluated the potential for fisheries-induced evolution of mating behavior and reproductive allocation in fish.
3. We used a unique experimental system of zebrafish (*Danio rerio*) lines exposed to large, small, or random (i.e. control) size-selective mortality. The large-harvested line represented a treatment simulating the typical case in fisheries where the largest individuals are preferentially harvested. We used a full factorial design of spawning trials with size-matched individuals to control for the systematic impact of body size during reproduction, thereby singling out possible changes in mating behaviour and reproductive allocation.
4. Both small and large size-selective mortality left a legacy on male mating behavior by elevating intersexual aggression. However, there was no evidence for line-assortative reproductive allocation. Females of all lines preferentially allocated eggs to the generally

less aggressive males of the random-harvested control line. Females of the large-harvested line showed enhanced reproductive performance, and males of the large-harvested line had the highest egg fertilization rate among all males. These findings can be explained as an evolutionary adaptation by which individuals of the large-harvested line display an enhanced reproductive performance early in life to offset the increased probability of adult mortality due to harvest.

5. Our results suggest that the large-harvested line evolved behaviorally-mediated reproductive adaptations that could increase the rate of recovery when populations adapted to high fishing pressure come into secondary contact with other populations.

KEYWORDS: aggression, egg fertilization, fisheries-induced evolution, reproductive isolation, zebrafish

INTRODUCTION

Many wildlife and fish populations are intensively harvested by humans. Harvesting represents an unnatural environmental pressure that has the potential to strongly shape the fitness landscape in exploited populations (Jørgensen et al. 2007). Indeed, exploitation of both fish and wildlife populations has been found to induce evolutionary adaptations in life-history and other traits over relatively short time scales (Heino et al. 2015, Alberti et al. 2017, Kuparinen and Festa-Bianchet 2017).

Fishing has been described as a large-scale experiment in life-history evolution (Rijnsdorp 1993) because it can be intensive and often size-selective (Jørgensen et al. 2007, Law 2007, Kuparinen and Festa-Bianchet 2017). Research on fisheries-induced evolution (FIE) has mainly focused on the evolution of life-history traits (Sharpe and Hendry 2009,

Devine et al. 2012, Heino et al. 2015). However, size-selective harvesting can also alter the physiology and behavior of fish populations (Walsh et al. 2006, Arlinghaus et al. 2017, Hollins et al. 2018), including mate choice patterns (Sordalen et al. 2018). Because nearly all phenotypic traits are at least modestly heritable (Mousseau and Roff 1987, Roff 2002, Dochtermann et al. 2015), harvest-induced trait change has the potential to foster the evolution of divergent mate choice patterns in exploited populations, which in turn can affect reproductive output (Rowe and Hutchings 2003, Dunlop et al. 2007, Sordalen et al. 2018). Indeed, selective harvesting can directionally change sexually-selected traits (e.g. Chiyo et al. 2015, Pigeon et al. 2016, Sordalen et al. 2018), but the role of sexual selection in FIE remains largely unexplored (but see Sordalen et al. 2018).

The fitness landscapes created by intensive and trait-selective harvesting could foster local adaptations in a manner similar to that of ecological gradients in eco-evolutionary contexts. Such scenarios are conceivable if meta-populations are exposed to differential fishing pressure and there is limited or no gene-flow among subpopulations (Alós et al. 2014). As such, the evolution of subpopulation-specific trait in response to selection gradients (e.g., those caused by different exploitation pressures) could even foster reproductive isolation barriers through sexual selection (Hendry 2004, Nosil et al. 2005, Hendry et al. 2007). Local adaptation can be facilitated by “magic” traits that are sexually-selected and contribute to non-random mating, reproductive isolation, and eventually speciation (Gavrilets 2004, Servedio et al. 2011). The contribution of sexual selection to early stages of ecological speciation has been demonstrated in several studies in which mate choice in fishes was affected by multiple ecological factors (Endler and Houde 1995, Langerhans et al. 2007, Seehausen et al. 2008). One of these factors is mortality associated with different predation regimes, which has for example been found to be responsible for

reproductive isolation driven by assortative mate choice in *Gambusia* (Langerhans et al. 2007). As such, it is plausible that mortality induced by fishing can produce similar evolutionary outcomes by favoring reproductive isolation driven by traits that are adapted to selective harvesting in different spatial units.

Sexual selection could also exert strong effects on FIE of phenotypic traits (Rowe and Hutchings 2003, Hutchings and Rowe 2008, Lane et al. 2011). In particular, phenotype-driven changes of the mating system (e.g. mate choice, dominance hierarchies or intrasexual competition; Lane et al. 2011) induced by intense fishing pressure and associated phenotypic changes in sexually-selected traits (e.g., body size or behavior) could affect: (i) the outcome of FIE; (ii) the speed, magnitude and direction of evolving traits; and (iii) population recovery (Dunlop et al. 2007, Hutchings and Rowe 2008, Enberg et al. 2009).

For example, Sordalen et al. (2018) demonstrated that size-selective fishing of large male European lobsters (*Homarus gammarus*) - the phenotype that naturally offers large fitness advantages - has the potential to attenuate sexual selection in fished areas, with a subsequent acceleration of FIE towards small male sizes. The authors suggest the creation of marine reserves to strengthen sexual selection and allow spillover of large males to exploited populations, so as to buffer FIE in exploited areas (Sordalen et al. 2018).

Unfortunately, we are not aware of any empirical studies that address the effects of size-selective harvesting on sexual-selection which in turn can affect reproductive performance in exploited fish populations.

We explored whether harvest-induced selection can foster the evolution of reproductive behavior using an experimentally-controlled system of zebrafish (*Danio rerio*) lines exposed to positive and negative size-selective harvesting (Uusi-Heikkilä et al. 2015). In earlier studies, the zebrafish selection lines have been found to differ phenotypically in

reproductive allocation (defined as the amount of energy allocated to reproduction; Lester et al. 2004), post-maturation growth and adult body size (Uusi-Heikkilä et al. 2015). Moreover, the selection lines differ genetically, in gene expression profiles and in personality traits (Uusi-Heikkilä et al. 2015, Uusi-Heikkilä et al. 2017, Sbragaglia et al. 2019a). In particular, the line in which large individuals were harvested (simulated trawl-like selectivity patterns or harvest regulations mimicking minimum-landing sizes) evolved a smaller body length, earlier age at maturity, higher relative fecundity, and a smaller maximum length compared to the control, suggesting evolution toward a fast life-history (Uusi-Heikkilä et al. 2015). In contrast, the line in which small individuals were harvested (simulating a harvest regulation mimicking a maximum-size limit or a gear with sharply reduced selectivity for very large individuals) evolved not only a different maturation schedule, but also reduced reproductive allocation compared to controls while maintaining adult sizes similar to the controls, suggestive of a slow life-history (Uusi-Heikkilä et al. 2015).

The fact that size-selective harvesting changed both adult size and behavior in the zebrafish model system is relevant from an assortative mating perspective. To isolate the behavior-driven mechanisms of mate choice, it is important to control for size because it is a key trait of sexual selection in zebrafish and other fishes (Pyron 2003, Nasiadka and Clark 2012, Uusi-Heikkilä et al. 2012a). Female zebrafish allocate reproductive resources depending on male size, usually favoring large and dominant males (Pyron 2003, Skinner and Watt 2007, Uusi-Heikkilä et al. 2012b). However, the reproductive allocation of female zebrafish may be reduced in the presence of extremely large males, probably due to an overt dominance and continued sexual harassment of females that is reproductively costly (Uusi-Heikkilä et al. 2012b, Uusi-Heikkilä et al. 2018). In fact, an important component for successful courtship behavior in zebrafish is the chemically-mediated inhibition of male

aggression by the release of ovarian pheromones by females (Hurk and Lambert 1983, Spence et al. 2008). In addition to size, male personality traits, including boldness and aggression, have been shown to affect offspring production and mate choice patterns in both zebrafish (Ariyomo and Watt 2012, Vargas et al. 2018) and other teleosts (Ariyomo and Watt 2013, Bierbach et al. 2015, Ibarra-Zatarain et al. 2019). In zebrafish, bold and aggressive (i.e., proactive) individuals have been found to reproductively outperform shy and less aggressive (i.e., reactive) fishes, independent of coloration patterns (Vargas et al. 2018). In guppies (*Poecilia reticulata*), females with similar personality to males have shown an elevated probability of producing offspring (Ariyomo and Watt 2013). Accordingly, fisheries-induced changes of reproductive behavior could affect reproductive output and lead to subpopulation-assortative mating, thereby contributing to fisheries-induced evolution of mate choice and possibly reproductive isolation.

To investigate whether size-selective harvesting can promote the evolution of mating behavior, we conducted size-matched spawning trials among the aforementioned lines of zebrafish. We examined the hypothesis that size-selection has altered the mating behavior of both size-selected lines and that these changes create a preferential mate choice for members of their own selection line. Accordingly, we predicted that during dyadic intersexual encounters (one male and one female), male aggression would be lower when both individuals were from the same selection line. Moreover, we expected that males of the line where small individuals were harvested would display lower levels of aggression and that males of the line where large individuals were harvested would display higher levels of aggression due to the correlation between life-history traits and aggression (i.e., the pace-of-life syndrome; Réale et al. 2010, Dammhahn et al. 2018). We focused our predictions on males because previous research has shown that male behavior, particularly male

aggression during spawning, is of key importance in zebrafish mating behavior (Spence et al. 2008, Vargas et al. 2018, Ibarra-Zatarain et al. 2019). We further predicted that patterns of line-assortative mate choice would manifest in greater numbers of eggs released and fertilized when zebrafish were crossed within the same selection line relative to being paired with any of the other two selection lines.

MATERIALS AND METHODS

Zebrafish selection lines

We used individuals from the F_{11} generation of the selection lines from Uusi-Heikkilä et al. (2015). We applied a strong directional selection pressures (a 75% per-generation harvest rate) acting on either large body size (large fishes harvested, as is typical for many fisheries; hereafter referred to as large-harvested line) or small body size (small fishes harvested as is possible in recreational fisheries, Pierce 2010, or in fisheries managed with a maximum-length limit; hereafter referred to as small-harvested line). We also applied a selection pressure randomly with respect to size (hereafter referred to as random-harvested line), representing a harvested control (Uusi-Heikkilä et al. 2015). Size-selection occurred during the first five generations, after which harvesting halted for six generations to remove any maternal effects and to facilitate the study of the evolutionary outcomes of selection using a common-garden approach (Uusi-Heikkilä et al. 2015). We firstly conducted analyses of life-history and lifetime growth at F_9 revealing that males and females in the large-harvested line evolved a smaller adult length and weight (Fig. 1) and higher relative fecundity compared to controls (Uusi-Heikkilä et al. 2015). By contrast, the small-harvested line showed reduced reproductive allocation and no change in adult length compared to the control line (Uusi-Heikkilä et al. 2015). Both size-selected lines evolved an alteration of the

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maturation schedule and matured at smaller sizes and younger ages than fish of the control line (for more details see Uusi-Heikkilä et al. 2015). These findings suggest a harvest-induced change in energy allocation. Any changes of basal life-history traits related to growth and maturation affect the post-maturation growth trajectory (Enberg et al. 2012). Although evolutionary rebound of key life-history traits from F_5 to F_{11} could happen and is reported in other selection experiments with different species (Conover et al. 2009, Salinas et al. 2012), among-generation assays of the growth trajectory using a Lester biphasic growth model (Lester et al. 2004, Honsey et al. 2017, Wilson et al. 2018) conducted at F_9 and F_{13} (see the Supplementary Material for details) showed that the selection lines maintained the evolved differences in life history and terminal length until F_{13} (Fig. 1). Thus, the evolved differences were almost certainly maintained at F_{11} (the generation used in the present work). Accordingly, we considered the large-harvested line to be characterized by a fast life-history and small terminal size compared to the control, and the small-harvested line by a slow life-history and a similar terminal size compared to the control.

We raised Individuals from the F_{11} generation in separate tanks in a common recirculation system until adulthood (~120 days post fertilization), after which we separated them according to sex-related morphological traits (Nasiadka and Clark 2012). Then, we anesthetized the fish with ethylene glycol monophenyl ether (Merck KGaA) at a dilution of 50-75 mg L⁻¹, placed them in a petri dish for measuring with a millimeter paper. After that we transferred the fish into acclimation aquaria (50 x 50 x 50 cm; water level 40 cm, no substrate) for at least three days before experimental trials. We used size-matched females ranging from 32 to 34 mm (standard length: mean \pm SD; 33.5 \pm 0.5 mm) and males ranging from 30 to 32 mm (standard length: 31 \pm 0.5 mm), to single out a possible impact of size-selection on behaviour and subsequent mating within and among lines. We used males that

were smaller than females because previous findings indicate that there are substantial reproductive costs related to males being too large relative to females (Uusi-Heikkilä et al. 2012b, Uusi-Heikkilä et al. 2018).

Male aggression during intersexual dyadic contests

To understand whether size-selection affected male behavior during spawning contexts, we created a full factorial design and examined all mating combinations among the three selection lines. We used eight replicates for each of the nine combinations. We randomly selected previously unfamiliar individuals (one male and one female) from the acclimation aquaria and housed them in five liter spawning boxes. We placed the boxes in the same recirculating water system under the following conditions: water temperature at 26 ± 0.5 °C; 10-14 h light-darkness cycle (light on at 07:00 am) and feeding with dry food (TetraMin, Tetra) and *Artemia* nauplii (Inve Aquaculture). We separated each box from the others by a white plastic divider to prevent visual contact. Additionally, we installed a cover shield at the front of each box that allowed scoring of behavior of one box without disturbing the others. To that end, we raised the divider and counted the number of agonistic interactions, i.e., bites (i.e., biting is the most common aggressive behavior in zebrafish; Paull et al. 2010). We counted the number of bites during five minutes after the first bite occurred. Within a given box, the two individuals were kept separated by a sponge for the first 24 hours. Agonistic interactions were then observed between 09:00 and 13:00.

Group spawning trials and reproductive allocation

To study outcomes of mate choice on reproductive allocation, we carried out a 4-day spawning trial between two females and four males, an assay that was used previously on

these lines (e.g. Uusi-Heikkilä et al. 2012a, 2012b, 2015). We used seven replicates for each of the nine combinations resulting from the full factorial design among the three selection lines. We used each group of fish only once, and we did not include the individuals already used for the aggression trials. The spawning trials took place in five liter spawning boxes placed in the same recirculating water system following the conditions reported above. Spawning in zebrafish occurs during the first daylight hours (Darrow and Harris 2004). Therefore, we removed eggs from the spawning boxes every day at 10:00 a.m. for four consecutive days, as was done in previous studies with these lines (e.g. Uusi-Heikkilä et al. 2012a, 2012b). We counted any collected eggs under a stereomicroscope and sorted them into fertilized and non-fertilized groups. We assumed that the total number of eggs released represented differential allocation by female zebrafish to preferred/non-preferred males (Spence and Smith 2006, Skinner and Watt 2007, Uusi-Heikkilä et al. 2012a), and we used the total number of fertilized eggs as a metric of reproductive fitness. We also recorded the fertilization rate, which can be affected by differential allocation of high or low quality eggs to males by females (Uusi-Heikkilä et al. 2012a), by sperm quality or by the ability of males to fertilize eggs (e.g., Watt et al. 2011).

Statistical analysis

We analysed the response variables with separate generalized linear models using a quasipoisson distribution for male aggression, total number of eggs and number of fertilized eggs, and a quasibinomial distribution for the proportion of fertilized eggs in relation to all eggs. We used quasi-distributions to account for overdispersion of the data. We tested for the effects of two categorical independent variables – female and male line – as main effects and interactions. Given the hypothesis-testing nature of our study, we used an

information theoretic approach (Johnson and Omland 2004). We selected the best fitting model using second order quasi Akaike Information Criteria for small sample sizes (qAICc) and corresponding model weights (Richards et al. 2011). Additionally, we used adjusted R^2 to quantify the proportion of explained variance by the independent variables. We ran all analyses using R version 3.4.3 (www.R-project.org/) with the additional package “MuMIn” (Bartoń 2014) for model selection and “rsq” (Zhang 2018) for calculating R^2 (Data are available here: Sbragaglia et al. 2019b).

RESULTS

Males displayed strong variation in number of bites, ranging from 0 to 181 during the 5-min trials. Reproductive performance was also highly variable in terms of total number of eggs (from 1 to 1246), number of eggs fertilized (from 0 to 380), and proportion of fertilized eggs (from 0 to 0.69).

Male aggression during intersexual dyadic contests was best described by the full model including the interaction between female and male line (Mod1 in Table 1). Male aggression and variability in male aggression were lowest when females from the small- and random-harvested lines were crossed with males of the random-harvested line (Fig. 2a). By contrast, male aggression was much higher when females from the random-harvested line were crossed with males from the large- and small-harvested lines, although variation was large (Fig. 2a). Despite substantial variation within each line, females from the large-harvested line experienced a lower level of male aggression than females from the other two lines (Fig. 3a). In addition, males from both the large- and small-harvested lines were generally more aggressive than males from the random-harvested line (Fig. 3b). These

results suggest that, in contrast to our hypothesis, size-selection altered male aggression in the same direction in both selection lines.

Despite evolutionary adaptation of male spawning behavior due to size selection, females did not release more eggs when paired with males of their own selection line, as indicated by the poor fit of the model that included an interaction term between female and male line (Mod6 in Table 1; Fig. 2b). Instead, the model with male and female line as additive effects was the best model (Mod7 in Table 1). This finding did not support our hypothesis of assortative mate choice within zebrafish lines leading to line-assortative reproductive allocation. Moreover, there were substantial differences in the number of eggs released across lines, as revealed by the significant main effects of female and male line (Table 1). Independently of which male was present, females from the large-harvested line released more eggs on average than females from the random-harvested line, while females from the small-harvested line released fewer eggs than females from the random-harvested line (Fig. 3c). Furthermore, females from all lines released fewer eggs when crossed with the more aggressive males of the large- and small-harvested lines than with males of the random-harvested line (Fig. 3d).

The total number of fertilized eggs and the percentage of fertilized eggs were also not systematically larger when males and females of the same line were paired together, as indicated by the poor fit of both models with interaction terms (Mod11 and Mod16 in Table 1; see also Figs. 2c and 2d). This finding further reinforced the idea that there was no line assortative reproductive allocation. Instead, the model with male line as the only explanatory variable performed best in explaining the total number of fertilized eggs, with the model with female line as an additional additive effect performing similarly well (Table 1). Specifically, males from the large-harvested line produced the largest number of

fertilized eggs (Fig. 3f). We also found a similar but weaker pattern in the females from the large-harvested line (Fig 3e). Finally, males of the large-harvested line fertilized a greater percentage of eggs than males of the small- and random-harvested lines (Mod19 in Table 1 and Fig. 3h), independent of the female line with which they were crossed (Fig. 3g).

DISCUSSION

We found that five generations of size-selective harvesting altered male aggression during intersexual dyadic encounters. However, we did not find evidence for assortative mating within zebrafish lines evolutionarily adapted to either large or small size-selective harvesting when engaging in size-matched spawning trials. Our results partially supported the first hypothesis that size-selective harvesting left a legacy in sexually-selected behavioural traits.

In particular, males of the random-harvested line were less aggressive when crossed with females of the small- and random-harvested lines, while females of the random-harvested line experienced considerably more male aggression when crossed with males of the large- and small-harvested lines. Our second hypothesis was not supported because we did not find evidence of line-assortative reproductive allocation. Instead, we found strong evidence for large- and small-harvested females releasing more eggs when paired with control (i.e., random-harvested) males. Moreover, our results showed that females from the large-harvested line produced more fertilized eggs, and males from the large-harvested lines fertilized a greater proportion of eggs, compared to the other two lines.

Previous studies showed that the zebrafish selection lines differed in personality traits such as exploration, boldness and sociability (Uusi-Heikkilä et al. 2015, Sbragaglia et al. 2019a). Our work adds to this research by showcasing that size-selection has altered male aggressive behavior during intersexual dyadic contests. In contrast to expectations, male

aggression increased in both size-selected lines and did not diverge as a result of the opposing directional size selection. The increased aggression by males of the large-harvested line agrees with the pace-of-life hypothesis (Réale et al. 2010, Dammhahn et al. 2018). Accordingly, the fast life-history is selected to reap fitness benefits early in life, such that males of the large-harvested line become more aggressive than controls, which has previously been shown to enhance reproductive success in zebrafish (Ariyomo and Watt 2012, Vargas et al. 2018). This interpretation cannot explain the high aggression level of males of the small-harvested line. We speculate instead that behavioral syndromes across life-stages (i.e., correlations of traits such as boldness, exploration and aggression; Sih et al. 2004, Conrad et al. 2011) could explain why males in the small-harvested line, which were found to be bolder as juveniles (Uusi-Heikkilä et al. 2015), were also found to be more aggressive than controls as adults.

Differential allocation of reproductive resources by females to preferred males has been repeatedly documented in zebrafish (e.g., Skinner and Watt 2007, Ariyomo and Watt 2012, Uusi-Heikkilä et al. 2012b). We found that females tended to release more eggs in the presence of males of the random-harvested line in a group spawning context (two females and four males). Males of the random-harvested line could be preferred by size-selected females and therefore receive more eggs because they were, on average, less aggressive in dyadic contexts compared to males of the large- and small-harvested lines. The presence of harassing males during courtship can increase female reproductive costs and may result in fitness costs to both males and females (Qvarnstrom and Forsgren 1998, Bierbach et al. 2013, Uusi-Heikkilä et al. 2018). In zebrafish, courtship behavior is usually characterized by a chemical inhibition of male aggression towards females (Hurk and Lambert 1983, Spence et al. 2008), and female reproductive allocation has been found to be reduced in the presence

of extreme large males (Uusi-Heikkilä et al. 2012b, Uusi-Heikkilä et al. 2018). It is possible that the small boxes and the maintenance of small groups over the four day period artificially elevated male aggression, in turn reducing the total number of eggs received by males from the large- and small-harvested lines.

We found that males from the random-harvested line were not always less aggressive than males from the other lines; in fact, their aggression increased when paired with females from the large-harvested line without a consistent decrease in the total number of eggs released by females. Thus, it remains unclear whether the increased reproductive allocation experienced by males of the random-harvested line was primarily driven by their lower aggression level or resulted from a combined effect of reduced aggression and other unmeasured male traits (e.g., coloration; Vargas et al. 2018).

Moreover, we found that the number of eggs released by females from the large-harvested line was greater than that of females from the other two lines, which could have contributed to our finding that males from the random-harvested line were more aggressive without reducing reproductive output when paired with females from the large-harvested line. An explanation for the elevated number of eggs produced by females from the large-harvested line could be that harvesting triggered the evolution of a fast life-history coupled with enhanced reproductive performance early in life (Uusi-Heikkilä et al. 2015; see also figure 1 and supplementary material), and females in turn released a greater number of eggs in order to reap fitness benefits early in life to offset the increased probability of adult mortality due to harvest.

We found that, when controlling for length, individuals from the large-harvested line (which represents the typical fisheries scenario with positive size-selective mortality) displayed enhanced reproductive performance (i.e., higher number and proportion of

fertilized eggs), independent of the other line that was involved in the spawning. These results can be interpreted as evidence for elevated reproductive fitness of the large-harvested line, which represents the life-history adaptation expected for exploitation contexts wherein large fish are selectively harvested (Jørgensen et al. 2007, Andersen et al. 2018). Different fertilization rates in relation to personality and size have been previously documented in zebrafish (e.g., Ariyomo and Watt 2012, Vargas et al. 2018), which can be both a function of females releasing eggs of differing quality based on perceived male quality and male performance (Ariyomo and Watt 2012, Uusi-Heikkilä et al. 2012a, 2012b). Both female and male traits are likely under selection and could have responded to five generations of intensive large size-selective harvesting (Uusi-Heikkilä et al. 2015, Baulier et al. 2017), providing two main explanations for our results. Firstly, as reported previously for these selection lines, the relative fecundity of females of the large-harvested line has been found to be the highest of all selection lines, indicating enhanced reproductive allocation (Uusi-Heikkilä et al. 2015). Similarly, we found that females of the large-harvested line deposited more eggs, which can lead to a higher number of fertilized eggs compared to the other lines. However, female line did not strongly affect the fertilization rate; thus, our results also suggest a further life-history adaptation by males of the large-harvested line in terms of ability to fertilize eggs. For example, males could have evolved specific traits that have been demonstrated to affect fertilization rate in zebrafish, such as keeping proximity to females during spawning contexts (Skinner 2004), elevated sperm quality (Paull et al. 2008), or improved ability to attract, guard and fertilize eggs via better maneuverability during spawning (Watt et al. 2011, Vargas et al. 2018).

Our results align with two studies that tested life history theory in response to size-selective harvesting in both experimental and field settings. Baulier et al. (2017) found that male (and, to a lesser extent, female) reproductive allocation increased during periods of high fishing mortality in Atlantic cod (*Gadus morhua*). Moreover, results from a size-selection experiment on guppies suggest that changes in reproductive allocation were particularly evident in males, but not in females (Diaz Pauli et al. 2017). Thus, the enhanced reproductive performance of the large-harvested line is likely caused by the evolution of a fast life-history that increased fecundity in females (i.e., number of eggs produced) and fertilization success in males (i.e., number and proportion of eggs fertilized). This interpretation is contingent on the assumption that the F_{11} lines used herein maintained key life-history adaptations to size-selective harvest observed in previous generations. We show that there is strong evidence to support this claim because the growth trajectories (and thus the underlying life-history traits related to reproduction, energy allocation and timing of maturation) reported by Uusi-Heikkilä et al. (2015) were maintained in the F_{13} generation (Fig. 1). Accordingly, the large-harvested line can be characterized as having a fast life-history (i.e., high reproductive allocation and reduced post-maturation growth) and the small-harvested line as having a slow life-history (i.e., low reproductive allocation and a large terminal length).

It is possible that some amount of recovery in traits that we did not measure has taken place after F_5 when we stopped the size-selection, and that such recovery could have influenced some of our findings. Nevertheless, our results suggest that the zebrafish selection lines maintained the previously-observed evolved differences in mating behavior, reproductive performance and life-history six generations after harvesting was halted. This aligns with selection experiments in other fishes that reported only partial recovery of

phenotypic traits after a period of highly intensive harvesting (Conover et al. 2009, Salinas et al. 2012). Another core aspect of our work that can be considered both as a strength and a limitation is that we used size-matched males and females. We did this in an effort to disentangle the effect of a behaviorally-mediated mechanism from size effects. However, in zebrafish and in many other species, body size is a key trait under selection (Pyron 2003, Uusi-Heikkilä et al. 2012a, 2012b). It is possible that the adaptations seen in our experiment in the large-harvested line could be reversed when the generally smaller individuals of this line meet with the larger members of the other two lines. Female preferences for larger males could then potentially reinforce fisheries-induced selection towards a fast life-history and small adult size as previously argued (Hutchings and Rowe 2008, Sordalen et al. 2018), rather than fostering population recovery via the enhanced reproductive performance of the large-harvested line documented here when body length was controlled. Further experiments without size-matched fishes have been initiated in our research group to explore this important question and to fully understand how the interaction between behaviorally- and size-dependent mate choices could contribute to the evolution of reproductive isolation of exploited populations in different harvesting scenarios.

Given that the selection lines we studied evolved different terminal sizes (Fig. 1), the standardization of size across selection lines implies that we used fish from the extremes of the size distributions of the different selection lines (upper percentiles for the large-harvested line and lower percentiles for the small-harvested line). Size variation within a cohort correlates with personality in zebrafish (Polverino et al. 2016). Therefore, we may have sampled different personalities from the selection lines, thereby possibly confounding our results. However, in a recent study we showed that the selection lines used here differ in personality traits (Sbragaglia et al. 2019a), but size variation across different cohorts did

not explain this personality variation. Therefore, it is unlikely that the size-matched approach used herein was substantially influenced by personality-biased sampling.

CONCLUSIONS AND IMPLICATIONS

Trait and population recovery (e.g., biomass recovery) following intensive size-selective harvesting have been repeatedly shown to be delayed due to FIE (Enberg et al. 2009, Neubauer et al. 2013, Dunlop et al. 2015). However, most of the published models have not explicitly considered mechanisms of sexual-selection, which have the potential to strongly influence FIE and its outcomes (Hutchings and Rowe 2008, Sordalen et al. 2018). Our results suggest that behaviorally-mediated reproductive isolation is unlikely in both positive and negative size-selective harvesting scenarios in the context of the model species that we examined. Furthermore, positive size-selective harvesting can lead to enhanced reproductive performance that, coupled with the absence of behaviorally-mediated reproductive isolation, could foster population recovery when exploited populations come into secondary contact with other populations (i.e. through stocking or dispersal from no-take reserves; Alós et al. 2014, Hessenauer et al. 2017). Because our conclusions are based on laboratory experiments on a single model species, we recommend further research including body size variation as well as multiple species comparisons to fully understand the interactions of fisheries-induced changes in mating behaviour and its impacts on sexual selection, reproductive isolation and population recovery.

AUTHORS CONTRIBUTIONS

RA and DB conceived and designed the experiment; CG and SUH acquired data; VS, CG, AEH and DB analysed data; VS, RA, DB and SUH interpreted the data; VS and RA wrote the article

with inputs by all other co-authors; all authors gave final approval of the version to be submitted.

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DATA ACCESSIBILITY

Data are available on Dryad Digital Repository: <https://doi.org/10.5061/dryad.181154k>
(Sbragaglia et al., 2019)

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Table 1. The models implemented in this study together with the second order quasi Akaike Information Criteria (qAICc), the difference in AIC between the best model and the other models (D), weight (W) and adjusted R^2 (Adj. R^2). The line in bold indicates the model used to interpret the results.

Response variable	Models	qAICc	D	W	Adj. R^2
Male aggression	Mod1: F line × M line	99.2	0.00	0.73	0.16
	Mod2: F line + M line	104.5	5.29	0.05	0.08
	Mod3: F line	109.9	7.90	0.00	0.00
	Mod4: M line	101.7	2.54	0.20	0.07
	Mod5: null model	107.1	10.65	0.01	-
Total number of eggs	Mod6: F line × M line	83.6	5.37	0.04	0.15
	Mod7: F line + M line	78.2	0.00	0.60	0.15
	Mod8: F line	81.7	3.47	0.11	0.10
	Mod9: M line	80.3	2.06	0.21	0.07
	Mod10: null model	83.7	5.52	0.04	-
Number of fertilized eggs	Mod11: F line × M line	86.7	10.58	0.00	0.05
	Mod12: F line + M line	77.2	1.05	0.22	0.09
	Mod13: F line	77.6	1.48	0.18	0.06
	Mod14: M line	76.1	0.00	0.37	0.03
	Mod15: null model	77.1	0.99	0.23	-
Proportion of fertilized eggs	Mod16: F line × M line	94.4	13.29	0.0	0.18
	Mod17: F line + M line	87.8	4.73	0.09	0.20
	Mod18: F line	103.8	20.67	0.00	0.00
	Mod19: M line	83.1	0.00	0.91	0.23
	Mod20: null model	99.6	16.50	0.00	-

FIGURES CAPTIONS

Figure 1. Sex specific differences in size (standard length expressed in mm, SL) and mass (wet mass expressed in g, WM) between generations F_9 (a, N = males: large-harvested, LH: 56; random-harvested, RH: 68; small-harvested, SH: 63; females: LH: 19; RH: 15; SH: 21) at 210 days post fertilization (DPF), F_{11} (b, N = 100) at 450 DPF and F_{13} (c, N = males: LH, 60; RH, 44; SH: 46; females: LH, 33; RH, 52; SH: 50). Fits of the Lester biphasic growth model (Lester et al. 2004) are also presented for generations F_9 and F_{13} (d). More details regarding the statistical approach are presented in the supplementary material.

Figure 2. Boxplots of the number of male bites to females (a; N = 8 per crossing), total number of eggs deposited by females (b; N = 7), total number of eggs fertilized (c, N = 7), proportion of fertilized eggs (d, N = 7). The full factorial design of the crossing among the selection lines is presented according to female and male line (large-harvested: LH; random-harvested: RH; small-harvested: SH).

Figure 3. The number of male bite to females according to female (a) and male (b) line (large-harvested: LH; random-harvested: RH; small-harvested: SH) when crossed with all the other lines (N = 24 by pooled sample). The total number of eggs deposited by females (c) and released to males (d) of each line when crossed with all the other lines (N = 21). The total number of eggs fertilized according to female (e) and male (f) line when crossed with all the other lines (N = 21). The proportion of fertilized eggs according to female (g) and male (h) line when crossed with all the other lines (N = 21).

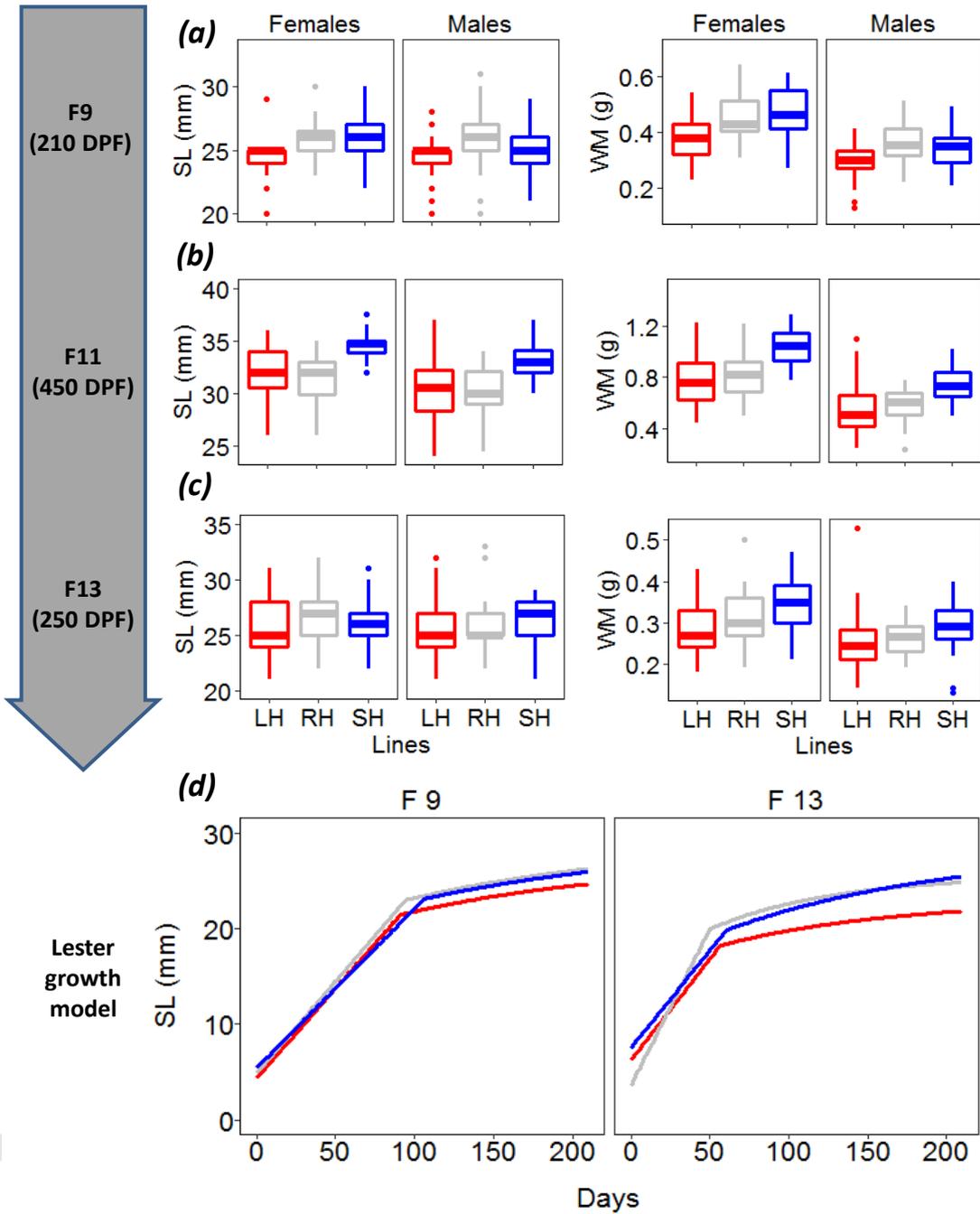


Fig. 1

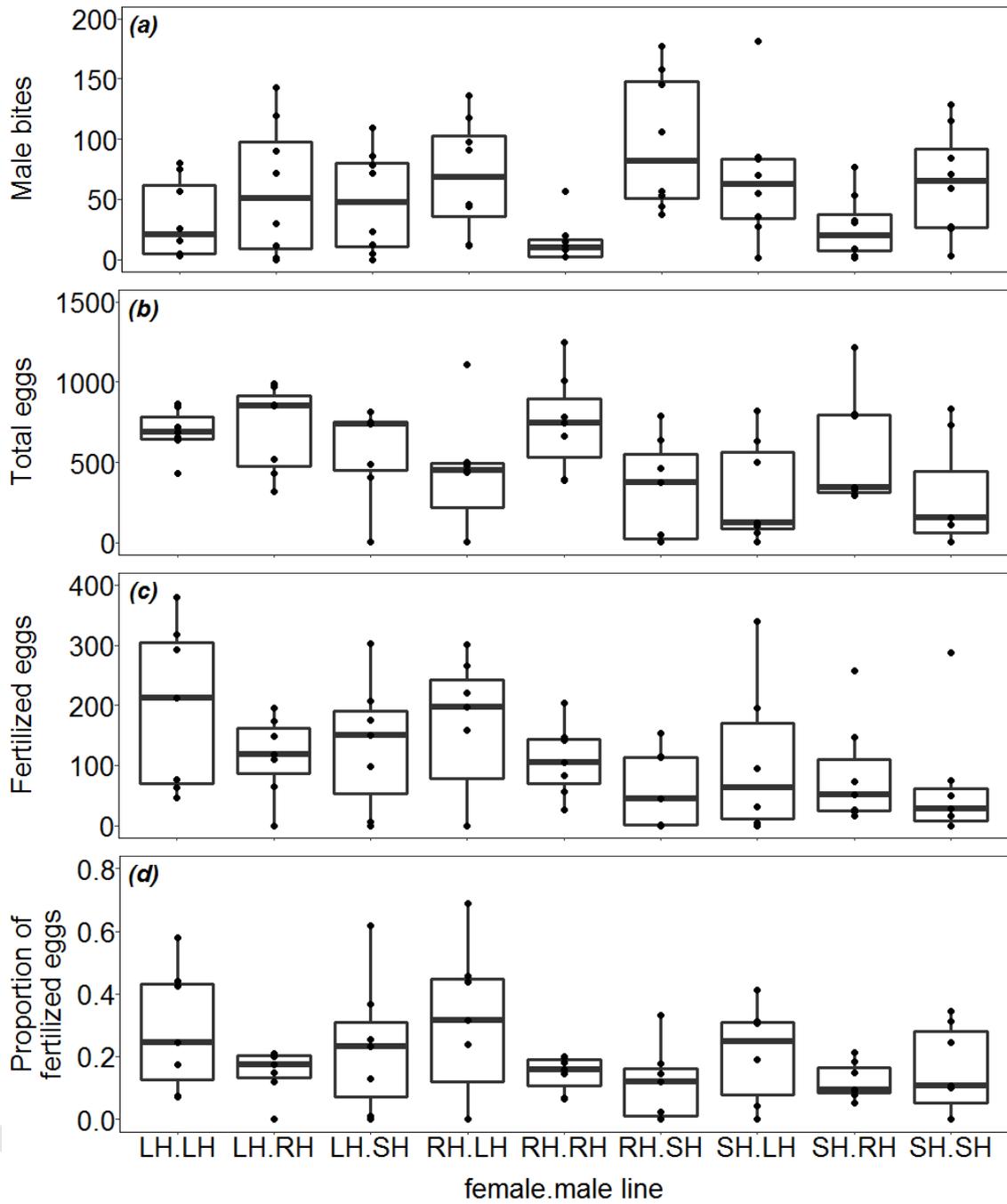


Fig. 2

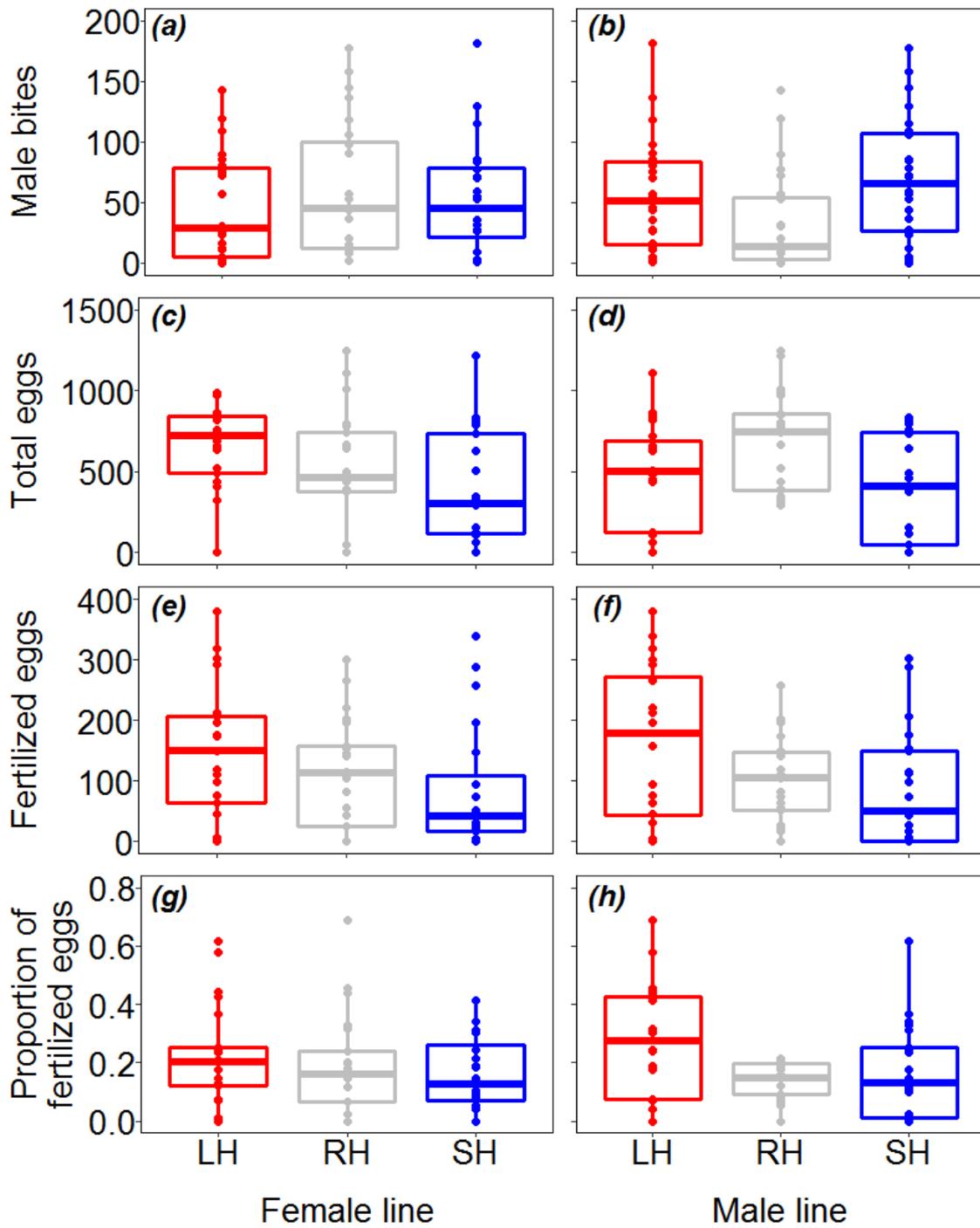


Fig. 3