Evolutionary biology

Altered trait variability in response to size-selective mortality

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Changes in trait variability owing to size-selective harvesting have received little attention in comparison with changes in mean trait values, perhaps because of the expectation that phenotypic variability should generally be eroded by directional selection typical for fishing and hunting. We show, however, that directional selection, in particular for large body size, leads to increased body-size variation in experimentally harvested zebrafish (Danio rerio) populations exposed to two alternative feeding environments: ad libitum and temporarily restricted food availability. Trait variation may influence population adaptivity, stability and resilience. Therefore, rather than exerting selection pressures that favour small individuals, our results stress the importance of protecting large ones, as they can harbour a great amount of variation within a population, to manage fish stocks sustainably.

1. Introduction

Intensive and selective removal of large individuals by fishers, hunters and plant harvesters can act as a pronounced directional selection force and decrease variation in natural populations [1]. Decreased trait variation can affect population dynamics and persistence in stochastically changing environments and communities [2]. Yet most studies on human-driven phenotypic changes disregard effects of harvesting on trait variation and instead focus on changes in mean trait values. Empirical and modelling studies, however, indicate that trait variation might show substantial responses to human-induced selection pressures [3–6].

Our study system consists of experimentally harvested zebrafish (Danio rerio) populations that were exposed to strong directional selection pressure (a 75% per-generation harvest rate) for either large body size (large-selected) or small body size (small-selected). A third line was harvested randomly with respect to size [7]. After five generations of size selection (followed by three generations of no harvesting to remove any ecological effects), the genetically diverged selection lines reared in groups and under ad libitum feeding differed significantly in their behaviour, reproductive investment and adult body size [7]. Here, we study whether the selection lines also differ in their size variation when reared under two contrasting environmental conditions.

We hypothesized that the large-selected fish maintain more size variation than the small-selected fish. First, large-selected fish included individuals that exceeded the 25% quantile, whereas small-selected fish included individuals
2. Material and methods

(a) Selection experiment design

We used wild-collected zebrafish and reared individuals in each generation in identical environmental and density conditions in the laboratory [7]. The three experimental populations originally consisted of 450 individuals per two replicated tanks. In the small-selected line, the 75% largest fish were harvested (mimicking selection typical of many fisheries [7]). In the large-selected line, the 75% smallest fish were harvested. In the random line, 75% of the fish were harvested randomly with respect to body size. The selection lines did not differ in their size variation at F1-generation (electronic supplementary material, table S1). After five generations of selection, harvesting was stopped for six generations before the size variation in the experimental populations was studied (more details in the electronic supplementary material).

(b) Growth experiment

The experimental fish were fed ad libitum with dry food and Artemia nauplii before they were first measured for standard length (SL) at age 35 days. Afterwards, fish from each selection line were transferred into individual rearing boxes to measure individual size-at-age. During the next 30 days all fish (13 individuals per selection-line replicate) were fed ad libitum with flake food. During this time (35–65 days) each individual was measured for SL every 10 days. To study the response in growth to temporary food limitation, nine boxes (i.e. individuals) per selection-line replicate experienced a dietary restriction (feed restriction) for 20 days while four boxes per selection-line replicate remained on ad libitum feeding (ad libitum). During the feed-restriction period, all fish were measured twice. At age 85 days, feed-restricted fish returned to ad libitum feeding, and fish from both treatments were measured every 5 days until the fish were 120 days old.

(c) Statistical analyses

We used three different statistical methods to quantify the differences in size variation, average body sizes and growth parameters among the selection lines. First, we used a linear mixed-effects model to test differences in the average size-at-age among the selection lines for each age class and both feeding treatments separately. Selection line was treated as a fixed effect and selection-line replicate as a random effect. Differences between the feeding treatments were also tested for each age class. Second, we used non-parametric methods to visualize differences in variation in size-at-age among the selection lines. We calculated the coefficient of variation (CV) for size-at-age for each selection line and both feeding treatments, and created a permuted distribution of CVs by assigning selection lines randomly among individual size measurements within each age class (repeated 10 000 times). The observed CVs for size-at-age of random, small- and large-selected fish were then compared with the randomly permuted distribution. Additionally, the age-specific CVs for size were bootstrapped 10 000 times to calculate the average CV and its 95% confidence intervals for each selection line in both feeding treatments. We then compared the averages of the distributions of the bootstrapped CVs (bootstrapped 50 times) among the selection lines using a linear model with bootstrapped CVs as a response variable and selection line as a fixed effect. Finally, to study mechanistic reasons for potential growth differences, we fitted a biphasic growth model [10] to the individual growth trajectories to extract the individual’s life-history traits, i.e. juvenile growth rate, age at the onset of maturation, reproductive investment and theoretical maximum body length (L∞, see the electronic supplementary material for details).

3. Results

In the ad libitum feeding, small-selected fish exhibited less size variation than large-selected fish throughout the entire experiment; they also exhibited less variation compared with the random line except at the very end of the experiment (105–120 days; figure 1a–d; electronic supplementary material, tables S2, S3). By contrast, large-selected fish showed a higher age-specific CV for size compared with the random fish at the end of the experiment (105–120 days; figure 1d, electronic supplementary material, tables S2, S3).

In the feed-restriction treatment, large-selected fish similarly exhibited consistently more variation than the small-selected and random fish. However, during the feed-restriction period the differences in variation between small- and large-selected fish disappeared (age 75 days; electronic supplementary material, figure S2, but see table S5) and generally eroded towards the end of the experiment (105–120 days; figure 1h, electronic supplementary material, figure S2, table S5). The small-selected fish initially were similarly variable in size as the random fish, but after 50 days they revealed greater variation than the random line (figure 1c–h; electronic supplementary material, tables S4, S5).

There were no consistent differences in average size-at-age among the selection lines in the ad libitum treatment (electronic supplementary material, table S2). Feeding restriction had a pervasive effect on average size-at-age in all selection lines, with no significant interactions among feeding treatment and selection line (electronic supplementary material, table S6). During the feed-restriction period (at ages 65 and 75 days), large-selected fish were significantly smaller than small-selected and random fish (electronic supplementary material, table S4). After the feed-restriction period (95–120...
Figure 1. (a) Individual growth curves of large-selected, (b) random and (c) small-selected fish in ad libitum feeding. (d) Bootstrapped average coefficients of variation (CV) and their confidence intervals in ad libitum feeding. (e) Individual growth curves of large-selected, (f) random and (g) small-selected fish in the feed-restriction treatment. (h) Bootstrapped average coefficients of variation (CV) and their confidence intervals in the feed-restriction treatment. Blue symbols indicate large-selected, grey random and red small-selected fish. Vertical lines indicate the feed-restriction period. The sample size was set slightly higher in the feed-restriction treatment because of the expected higher size variation.

Figure 2. Permuted coefficient of variation (CV) distributions for each age class in ad libitum treatment. Observed age-specific CVs of large-selected fish are marked in blue, random fish in grey and small-selected fish in red. Black bars indicate the 95% quantiles of the permuted data.
days), random fish were, on average, larger than small- and large-selected fish (electronic supplementary material, table S4). There were no differences in the model-estimated average juvenile growth rate (electronic supplementary material, figure S2a), age at the onset of maturation (electronic supplementary material, figure S2b), reproductive investment (electronic supplementary material, figure S2c) or $L_w$ (electronic supplementary material, figure S2d) among the selection lines in either the ad libitum or feed-restriction treatments.

4. Discussion

We demonstrate largely consistent differences in size variation among large-selected relative to small-selected and random fish in two contrasting feeding treatments. This suggests that size selection, particularly for large body size, generally fostered size variation but our results also highlight a moderating effect of the food environment on trait expression as the differences in variation between small- and large-selected fish started to erode after the feed-restriction period. Furthermore, differences in trait variation among the selection lines were less pronounced under ad libitum feeding; while under restricted feeding, size variation of both size-selected lines was higher than variation among the random fish. The size-variation difference decreased after the feed-restriction period among the selection lines potentially because the nutritional stress forced the fish to follow similar growth trajectories. However, the size-variation difference was still 5–10% lower in random and small-selected fish compared with the large-selected fish, particularly at the beginning of the experiment. A quantitatively similar decrease in size variation (5–10%) has been shown in a population under fish-induced disruptive selection.

We found that the large-selected fish exhibited higher trait variation compared with the small-selected fish despite both having experienced intense directional selection. While fish can reach similar or even identical sizes-at-age using vastly different behavioural strategies [11], it is plausible that selection for large body size maintained more variation in underlying physiological or behavioural traits that contribute to large size than was possible among the small-selected fish. Hence, the large-selected fish were able to express more size (and growth) variability at the population level (particularly in ad libitum feeding), which could be a consequence of increased phenotypic plasticity for these traits. Also, the selection lines vary in their personality [7], and personality traits are systematically related to stress responsiveness and coping styles [9]. Environmental stress is known to foster trait variation in zebrafish [8] and, therefore, for physiological and behavioural reasons the size-selected lines possibly responded more strongly to food-induced environmental stress than the random line, elevating trait variability without a corresponding change in mean trait values.

5. Conclusion

Focusing on detecting changes in mean trait values in response to harvesting provides an incomplete picture of the phenotypic, and potentially evolutionary, effects of size selection. While phenotypic variation has largely been ignored in studies detecting and investigating harvest-driven evolution (but see [3–6]), it is increasingly recognized that intraspecific variation can have a profound influence on population and food-web dynamics [2]. Altered trait variability caused by harvesting can affect a population’s capacity to disperse—to buffer environmental change—the rate of evolutionary rebound and ultimately population recovery from exploitation [2]. Given our findings of increased trait variation among large-selected fish, regulations that protect large individuals in exploited stocks could be a better management strategy than the ones that foster the selective removal of large fish.

Ethics. All procedures were approved by the Animal Experiment Board in Finland (approval no. ESAVI/2597/04.10.07/2013).

Data accessibility. Data are deposited in Dryad: http://dx.doi.org/10.5061/dryad.410fc [12].

Authors’ contribution. S.U.-H., A.K. and K.L. conceived and designed the experiment. A.K. and J.A. analysed data. R.A. helped to interpret the data, S.U.-H., A.K. and R.A. drafted the article, and K.L., N.P. and J.A. revised it critically for important intellectual content. All authors gave final approval of the version to be published and agreed to be accountable for all aspects of the work.

Competing interests. The authors declare no competing interests.

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References


10. Lester NP, Shuter BJ, Abrams PA. 2004
