

Phenotypic and genetic changes in life history traits in experimental populations of guppies (*Poecilia reticulata*) that experienced size-selective fishing

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Summary

In this study nine experimental populations of Trinidadian guppies, *Poecilia reticulata*, were subjected to size-selective harvest in order to study adaptive and phenotypic responses of fishing. We compared three different fishing regimes: 1) *positive size-selective harvest*, where individuals larger than a minimum size (16 mm) were killed, mimicking a commercial fishery; 2) *negative size-selective harvest* consisted of removing individuals smaller than 16 mm; and 3) in *size-independent harvest* both large and small individuals were killed. The experimental populations were self-renewing, with overlapping generations, allowing for ecological feedbacks, and natural and sexual selection. Harvesting took place every six weeks. After 3.1 years (4.3 generations on average) of selective harvest we observe phenotypic reduction of the length at maturation in *positively harvested* populations, probably due to size-selective harvest. In addition, we studied genetic changes with a common garden experiments (before and after 3 years of selection) and with molecular analysis (comparing populations after selection). Preliminary results show that individuals in all populations have higher odds to mature after 3 years of selection, but the increase seems higher for fish that experienced positive size-selection relative to those experiencing size-independent harvest.

Introduction

Fishing increases mortality and reduces chances for future reproduction, thus adaptation to earlier reproduction is expected. In addition, fishing is purposely selective towards larger, more profitable individuals, favouring early reproduction even more. If the phenotypic variation in the selected traits has some genetic basis, then fishing should induce genetic changes, i.e., evolution (Law 2000). Life history traits are known to be heritable (Merilä and Sheldon 2000), and many methods have been developed to study the evolutionary effects of fishing: 1) theoretical models designed to study the effect of fishing on a range of life history traits, rate of change and of reversal, 2) statistical methods to infer genetic changes from phenotypic life history data, and 3) common garden and selection experiments to disentangle genetic from environmental differences, control selection differentials and estimate rate of change. However, there is still no conclusive proof that selective fishing is causing genetic changes in the wild, thus the occurrence of fisheries-induced evolution is under debate. The main criticisms posed to the current studies of fisheries-induced evolution can be summarized as 1) the lack of direct genetic evidence for the observed phenotypic changes (Kuparinen and Merilä 2008), 2) exaggerated fishing selectivity compared to real fishing pressure (Brown et al. 2008), 3) unrealistic experimental conditions that do not resemble natural populations (Hilborn 2006), and 4) lack of considering the role of environmental drivers (Browman et al. 2008; Andersen and Brander 2009). The unrealistic experimental conditions refer to populations with discrete generations, absence of density feedbacks and natural selection, and use of model species too different from typical commercially exploited fish.

We aim to circumvent some those limitations with a selection experiment on age- and size-structured populations with overlapping generations, in which ecological feedbacks and natural and sexual selection are permitted to take place. Our populations present iteroparous life history and they are exposed to intensities mimicking the commercial fishing selectivity and mortality, which make them more comparable to typical exploited species. The more complex experimental set-up allows for unanticipated selection responses that may accelerate or retard the rate of evolution due to exploitation (Hutchings and Rowe 2008). Our model species is the Trinidadian guppy, *Poecilia reticulata*. While obviously different from fisheries stocks, we believe that our experiment has the ecological realism lacking in previous studies, which makes it more comparable to commercially exploited populations.

Materials and Methods

Nine experimental replicate populations of Trinidadian guppies, *Poecilia reticulata*, were harvested every six weeks with one of the three different fishing regimes for three years. The fishing treatments were: 1) *Positive harvest* was positively size-selective and consisted of removing proportion P (25%, 33% or 50%, depending abundance) of the individuals larger than 16 mm standard length, 2) *Negative harvest*, with negative size-selection, removed P of the individuals smaller than 16 mm SL

(approximately $P/2$ of the whole populations), and 3) *Random harvest*, $P/2$ of all the individuals were removed irrespectively of size. Each treatment was replicated three times. The size threshold for harvesting was chosen because males and females begin maturing typically around 16 mm SL. The experiment lasted three years, which is 4.5 guppy generations on average (3.8, 4.0 and 5.6 generations in negative, random and positive harvests, respectively). During each harvest event, we sampled a representative 25% of the population to obtain data on length, weight, and maturation stage and, once a year, fecundity. In addition, once a year we sampled four females from each population that were reared in common garden conditions. We reared their F2 offspring and assessed growth, maturation and fecundity from them. Differences that persist when populations are reared in identical conditions suggest a genetically heritable basis to the variation.

Results and Discussion

Phenotypic trends

1) *Male maturation* fluctuated over the three years of experiment. However, males from population where large individuals were fished out presented lower length at the end of the experiment, relative to males from negative harvest treatment. The rate of change in Haldanes estimated from the whole time series showed a significant decrease in length at maturation for males in positive harvest ($h_p(0.75) = -0.00009$ (CI, -0.0002 – -0.00000008), $p = 0.05$) and random ($h_p(0.60) = -0.0001$ (CI, -0.0002 – -0.00009), $p = 0.00003$) treatments, while there was no change on negative harvest treatment ($h_p(0.58) = 0.00001$ (CI, -0.00005 – 0.00007), $p = 0.73$). In the end of the experiment, L50 (length at which 50% of the males are mature) significantly differed between the treatments. Males from positive harvest presented lower L50 relative to males in negative harvest.

2) *Female maturation*, only assessed from three annual samples, differed between treatments. L50 from positive and random harvest decreased over time, while it did not change in negative harvest.

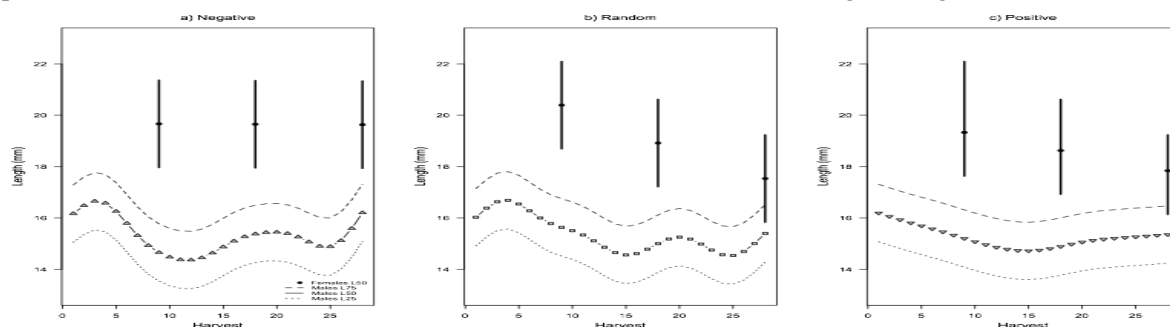


Figure 1. Curves represent L50 (solid with grey triangles and squares), L25 (dotted) and L75 (dashed) for males from samples in each harvest. These are the lengths at which the probability of being mature is 50%, 25% and 75%, respectively. The round dots represent L50 for females at three harvest events and the thick solid lines illustrate the length interval within which the probability of being mature increases from 25 to 75%.

Genetic changes

Here F2 individuals reared under common garden conditions representing the populations before harvest (first assay) and after two years of harvest (second assay) were compared.

1) *Male maturation* did not differ between fishing treatments in F2 fish reared under common garden conditions. However, all males had lower probability of maturing (higher L50s) after two years of harvest compared to prior size-selection. This suggests adaptation to the experimental conditions.

2) *Female maturation* differed between fishing treatments after two years of harvest. Females from the positive harvest treatment and the second assay presented higher probability of maturing with increases in age.

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