Size-selective harvesting alters biological traits of marine medaka (*Oryzias melastigma*)

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Under long-term fishing pressure, the biological traits of many wild fish populations have changed. Such phenotypic changes include smaller in size and earlier age-at-maturation, strongly suggesting that fishing could induce rapid changes in the life-history traits of fish. However, whether extensive fishing will lead to genetic changes in fish, how they occur, and whether they are reversible still requires further research. In this study, we analyzed biological traits of marine medaka (*Oryzias melastigma*) subjected to 50% experimental harvest for 4 consecutive generations. This study adopted a factorial design with three size-selective harvesting strategies (large-, small-, and random-size selection) on groups either before or after maturation. We compared the growth, maturation, and early life stages of marine medaka for different harvesting strategies. The results showed that the mean lengths and mean weights in large-harvested populations significantly declined after 4 generations, whereas small-harvested populations did the opposite. Furthermore, selective harvesting of large individuals also led to earlier maturation, declining fecundity, declining hatching rate and increasing larval mortality. Importantly, compared to harvesting before maturation, harvesting after maturation could mitigate the effects of harvest on biological traits. This study provided experimental evidence for the impact of selective harvest on phenotypic evolution and contributed to the theoretical basis for sustainability in fisheries and fishery management.

1. Introduction

Wild populations have rapidly evolved in the modern age, due to human activities such as fishing (Allendorf et al., 2008; Conover et al., 2009; Jorgensen et al., 2007). The fishing industry often seeks to harvest larger individuals, and to repeatedly harvest in areas with high biomass. These high-intensity and selective fishing activities have led to problems such as overfishing and contributed to a decline in fishery resources. Moreover, the phenotypic traits of many wild populations have changed over the past few decades, as evidenced in the smaller body size and earlier age-at-maturation of some species (Allendorf and Hard, 2009; Bobko and Berkeley, 2004). This mechanism is confirmed in a variety of commercial species under high-intensity fishing, using fishing gears such as gill nets, trawls, and commercial trolls, which always remove larger fish than the average size (Jorgensen et al., 2009; Pardoe et al., 2009; Ricker, 2011; van Walraven et al., 2010). In China, important commercial stocks like small yellow croaker (*Pseudosciaena polyactis*) and largehead hairtails (Trichiurus japonicus) have also seen similar changes (Lin et al., 2004; Ji et al., 2019; Sun et al., 2020).

Responding to the detrimental effects caused by fishing, a series of management strategies have been implemented in China, such as the closed season policy, defined as "the period during which the taking of fishing activities is prohibited in specific areas (Yu et al., 2007). However, due to the high diversity of life cycles, it is difficult to define a closed season that covers all of the species, resulting in some species still being caught before maturation. For example, the closed season begins on May 1 in the South China Sea, while the juvenile growth period of many species is generally from April to May, such as chub mackerel (*Scomber japonicus*), round scad (*Decapterus maruadsi*) and anchovy (*Anchoviella commersonii*). Juveniles have even been reported as the leading composition of trawling catches (Feng et al., 2019). To a certain extent, the limited effectiveness of the policy could lead to immature fishing on specific species (Feng et al., 2019; Yan et al., 2019; Zhou, 2007), resulting in changes of age and size composition of fish groups. Consequently, the reproductive potential and population dynamics would also be influenced, as most species exhibit a size-dependent fecundity (Ernande et al., 2004). For example, Yan et al. (2007) re- ported that after the end of the closed season, the number of immature hairtails in the East China Sea was still large, and mesh size of the fishing gear was small, making it difficult to release the juveniles. In the next spawning period, there were fewer parents, and the population was still small in size. The catch quality was not fundamentally improved. Hence, not only does selective fishing influence the biological traits of populations, but fishing at different times is also a potential contributing factor.

Presently, studies on fishing-induced phenotypic changes in fish are mainly based on empirical fishery resource surveys, theoretical modeling, experiments, and genomic research (Conover and Munch, 2002; Conover and Baumann, 2009; Dercole and Rossa,

2017; Pardoe et al., 2009; Therkildsen et al., 2013; Uusi-Heikkilä et al., 2017; van Walraven et al., 2010). Experimental harvesting experiments in the laboratory can standardize environmental factors and fishing pressure, and clearly attribute the phenotypic and genetic changes to fishing pressure (Renneville et al., 2020). Size-selective harvesting experiments have shown that population changes correlate with the directions of harvesting strategies. For example, an experiment on the Atlantic silverside (*Menidia menidia*) showed that size-selective harvesting can lead to population yield changes greatly under different fishing strategies, with low recovery rates after harvesting stopped (Conover and Munch, 2002; Conover et al., 2009). Size-selective harvesting can also make the length of male guppies (*Poecilia reticulata*) in small-harvesting populations longer than the large-harvesting populations (van Wijk et al., 2013). Zebra fish (*Danio rerio*) showed more reproductive investment and smaller body size in large-harvesting populations (Uusi-Heikkilä et al., 2015). And Amaral and Johnston (2012) found that large-harvesting could lead the egg and yolk diameter of zebra fish declination.

The experimental subject of harvesting experiments usually chose model organisms because of their representativeness and short life history. As a common model organism, marine medaka (*Oryzias melastigma*) have the advantages of oviparity and can adapt to a wide range of temperatures and salinities. They also have a short generation time (2–3 months) with spawning possibilities only 60 days after hatching (Park et al., 2019). Moreover, they are small in size, have high fecundity, have transparent eggs, and exhibit distinct sexual dimorphism. (Dong et al., 2014; Inoue and Takei, 2002; Kong et al., 2008). In addition, sequence and analysis of medaka genomes have been established (Kasahara et al., 2007), which makes it possible to study the fishing-induced evolution at the molecular level.

There have been many experimental studies to explore the effects of size-selective harvesting on fish. However, the influence of different harvesting times is seen in a limited number of reports. In this study, the marine medaka was chosen as an experimental subject to reveal the impact of harvesting strategies and times. We performed harvesting experiments at two different harvesting times: before and after maturation. The objectives of this study are to (1) investigate the effects of size-selective harvesting on biological traits and the early life stages of marine medaka and (2) determine the differences between two kinds of harvesting times in the populations. This study could provide an experimental reference for studying phenotypic trait changes using different harvesting strategies and times. It could also provide suggestions for fishery management, such as more accurately determined closed season and fishing times.

2. Materials and methods

Breeding and harvesting design

We selected marine medaka as our experimental species. The marine medaka were originally provided by the State Key Laboratory of Marine Environmental Science, Xiamen University (China), and have been maintained at the Ocean University of China since 2016. Before the experiment, we bred medaka for two generations to gain information and refine the experimental design. Because females have shorter and more regular anal fins, individuals can be sexed based on the differences in anal fin size (Im et al., 2016). We found that marine medaka can be sexed at approximately 55 days post-hatch and that spawning first occurs approximately 70 days post-hatch. In this study, we assumed that the distinguishing ability of sexes coincides with sexual maturation, and innovatively designed 40 days post-hatch or 60 days post-hatch as the fishing time. The time points corresponded to harvesting before maturation or after maturation in the initial population. Inclusively, both harvesting times occurred before spawning.

The experiment was initiated with 1080 marine medaka from different families as the parental (F0) generation, which was then divided into 18 populations and bred for four generations (F1-F4) while subjecting them to experimental size-selective harvesting strategies.

The experiment followed a factorial design (Fig. 1), where size- selective harvest treatment (three levels) was crossed with the timing of the harvest treatment (two levels). The size-selection treatment followed earlier studies (Amaral and Johnston, 2012; Conover and Munch, 2002; Therkildsen et al., 2019): either the largest 50% were harvested (large-harvested, LH), a random 50% were harvested (random-harvested, RH), or the smallest 50% were harvested (small-harvested, SH), with the remaining 50% marine medaka then being used for reproduction. Therefore, we had six treatment combinations, which we denoted as LH40, RH40 and SH40 (harvesting on 40 days post-hatch) and LH60, RH60 and SH60 (harvesting on 60 days post-hatch). There were three populations in each treatment combination.

In this study, the juvenile and adult fish were cultivated in a recirculating aquaculture system with constant temperature (26–28 ∘C) and salinity (30 ppt). The fish experienced a 14:10 (light: dark) photoperiod and were fed with the nauplii of brine shrimp (*Artemia sinica*) twice daily. The eggs and larvae were placed in petri dishes and cultured in a light incubator at 30 ℃ and 5000 lx light intensity. They also experienced a 14:10 (light:dark) photoperiod and were fed cooked egg yolk powder. When the larvae reached the first feeding time, they were transferred to the 192-liter aquaria in the recirculating aquaculture system.

Trait measurements

In this study, we explored both maturation and spawning under different harvesting strategies and times. This is because maturation is one of the important life history characteristics of fish, and reproduction is crucial for population supplement. We observed the experimental populations daily to determine the age at which sexes became visually separable (henceforth referred to as the age at sexual differentiation) and the age at which spawning started (henceforth referred to as the age at first spawning).

We recorded the number of females in each population at 60 days post-hatch. The number of females in each population were mostly between 32 and 35. To mimic a natural set-up, the spawning in this study was a mass spawning. Twenty days after the first spawning, we started to collect the eggs. We recorded the spawning amount within 30 days. In this study, we calculated fecundity as:

fecundity = Total number of eggs/ the number of females

And we recorded the number of hatching larvae. The hatching rate of eggs was calculated as:

hatching rate = number of newly hatched larvae/number of eggs×100%

2.1. Data analysis

For each population (18 in total), we randomly selected 300 larvae from the same batch, and divided them into three equal-size groups of 100 larvae. We recorded the number of daily deaths until five days post- hatch and calculated the mortality rate over five days. Larval mortality was estimated as:

larval mortality = number of deaths over 5 days in each group/original quantity of larvae in each group×100%

When the larvae reached the first feeding time, 130 individuals selected randomly from each population were transferred to the recirculating aquaculture system.

We postulated that large-harvesting before maturation may lead to greater changes in maturation than post-maturation harvesting. To explore more information about fish before harvesting, we designed an earlier time for pre-maturation populations to measure the length and weight. They were measured on 30, 40, and 60 days post-hatch in the pre-maturation harvest populations and on 40 and 60 days post-hatch in the post-maturation harvest populations. The body size of each fish was measured using the total length of the fish. Each fish was photographed with a camera, and the total length of the fish was measured by calibrating the image with a fish measurement system. At the time of fishing (9 populations harvested on 40 days post-hatch, another 9 populations harvested on 60 days post-hatch), the measured body length will be sorted by size. And we selected 50% of the fish according to three harvesting strategies. Their weights were measured using an

analytical balance (nominal precision calibrated to one ten-thousandth of a gram). The minimum accuracy of total length and weight was 0.1 mm and 0.001 g.

All of the data were conducted for the Normality Test by Shapiro- Wilk test, and the data were normally distributed. Besides, the replicate populations were conducted by one-way ANOVA, and there were no differences. Therefore, in this study, the data were summarized as the mean standard deviation (SD) in each treatment. Statistical analyses were conducted by two-way ANOVA and multiple testing to explain the differences between the three harvesting strategies and two harvesting times and the interaction between selection line and harvesting times. All analyses were carried out with the "shapiro.test", "aov" and "Tukey HSD" functions in R. The results were recorded and graphed using Microsoft Excel 2016.

3. Results

Maturation

Age at sexual differentiation

Significant differences in age at sexual differentiation were found among three size-selective harvesting strategies ($P < 0.01$) and different harvesting times ($P = 0.0122$) (Supplemental Tables S2): large-harvested populations reached sexual differentiation significantly earlier than fish in other size-selective treatments, and the populations harvested before maturation changed more than those harvested after (Fig. 2). In large-harvested populations that harvested before maturation, it was 16.67 days earlier than that in random populations and 6.33 days earlier than harvested after maturation (Supplemental Tables S1). The age in small-harvested populations showed a first increasing then decreasing trend and was nearly constant in random-harvested populations. The difference between these two treatments can be ignored ($P = 0.2817$) (Supplemental Tables S2).

Age at first spawning

The age at the first spawning also changed obviously among the three treatments ($P < 0.01$) (Supplemental Tables S4). It showed a slowly increasing trend in small-harvested populations, and a decreasing trend in large-harvested populations (Fig. 3). For the pre-maturation harvest populations, compared to random populations, it was 22.66 days earlier and 2.67 days later in the large- and small-harvested populations (Supplemental Tables S3). Based on these results, post- maturation harvesting could be identified as a mitigating factor regarding these changes (Fig. 3). The difference between the different harvesting times was also significant (P 0.000451) (Supplemental Tables S4).

Fecundity

Selective fishing also led to great changes in fecundity. The large- harvested populations decreased dramatically, while the small- harvested populations increased (Fig. 4). The fecundity in large- harvested populations fished before maturation was only 54.1% of that in small-harvested populations (Supplemental Tables S5). Post-maturation harvesting populations produced higher fecundity. The differences among the three size-selective treatments and two kinds of times were both significant markers supporting these theories (P < 0.01, Supplemental Tables S6).

Hatching rate

The hatching rates declined during 3 generations and showed a rate of faster declination in large-harvested populations and slower declination in random populations (Fig. 5). In generation 3, the differences among the three treatments were significant (p < 0.01) (Supplemental Tables S8). In large- and small-harvested populations that harvested before maturation, the hatching rates were 16.95% and 10.11% lower than in random populations, respectively (Supplemental Tables S7). Additionally, there was no significant difference between populations at different fishing times (p = 0.743) (Supplemental Tables S8).

Larval mortality

Large changes in larval mortality were observed. Said observations displayed rapid increases in large-harvested populations across three generations and a pattern of decline in small-harvested populations (Fig. 6). In generation 4, the larval mortalities were meaningfully different among the three strategies (P < 0.01) and the two kinds of fishing time (p 0.0277) (Supplemental Tables S10). The three treatments of large-, random- and small-harvesting in post-maturation harvesting populations were 2.11%, 0.89% and 2.78% lower than in pre-maturation harvesting populations, correspondingly (Supplemental Tables S9).

Length

Across four generations, the mean lengths changed noticeably among the three treatments (P < 0.01) (Supplemental Tables S12). It showed a decreasing trend in large-harvested populations and an increasing trend in small-harvested populations (Fig. 7). In this study, we compared the mean lengths at 40 days post-hatch of the populations from two harvesting times. The changes were more obvious in the populations harvested before maturation (Fig. 7). For pre-maturation harvesting populations, the mean lengths in large-harvested populations were 0.7 and 1.8 mm shorter than random- and small-harvested populations. For the post-maturation populations, the mean lengths in large-harvested populations were 0.3 and 0.9 mm shorter (Supplemental Tables S11), with the difference being negligible during different harvesting times (P = 0.1052) (Supplemental Tables S12).

Weight

Weight changing trends paralleled length trends. Reviewing the results of the 40 days post-hatch, there were major differences among the three treatments (P < 0.01) (Supplemental Tables S14). The average weights of each subsequent treatment were 0.020, 0.026 and 0.029 g in populations harvested before maturation (Supplemental Tables S13). The changes were smaller in the groups harvested after maturation (Fig. 8), but the differences in the two kinds of harvesting times were minuscular (P = 0.0918) (Supplemental Tables S14).

4. Discussion

This experimental approach in marine medaka demonstrated changes in length, weight, age at sexual differentiation and first spawning, fecundity, hatching rate of eggs, and larval mortality in response to four generations of size-selective harvesting. The results also showed the differences between different times of harvesting.

Effects of size-selective harvesting on marine medaka population traits

Summarily, the length of marine medaka changed profoundly in four generations. For the populations harvested before maturation, the average length in the large-harvested populations was 1.8 mm smaller than that in the small-harvested populations, and the average weight was 0.009 g less at 40 days post-hatch (Supplemental Tables S11, 13). This result was consistent with other size-selective fishing experiments. The body size of Atlantic silverside in the small-harvested lines was 25% longer than fish from the large-harvested lines, and the average weight doubled (Conover and Munch, 2002; Therkildsen et al., 2019; Walsh et al., 2006). The difference between large-harvesting lines and small-harvesting lines in other species was 3 mm in mature male guppies (van Wijk et al., 2013) and 2.1 mm in zebra fish (Uusi-Heikkilä et al., 2015). For medaka fish (*Oryzias latipes*), the differences between small- and random-harvesting populations were 1.5 mm (Renneville et al., 2020). The changes in body size were attributed to fishing (Marty et al., 2015; Sharpe and Hendry, 2009; van Walraven et al., 2010). It could be explained by the energy conversion mechanism and energy allocation mechanism. All organisms should allocate energy to growth, reproduction, maintenance, and storage (Enberg et al., 2012; Heino and Dieckmann, 2009), and the resources are finite (Reznick et al., 2000). To adapt to fishing pressure, many stocks allocate more energy to maturation and reproduction. It is conducive to the continuation of the populations. When the energy used for growth is reduced, the growth rate slows down. In our study, for the pre-maturation harvesting populations, the mean lengths of marine medaka in small-harvested lines increased by 3.2 mm from 30 dph to 40 dph, while that in the large-harvested lines only increased by 2.7 mm (Supplemental Tables S11), and the growth rate was significantly lower. The changes in growth rate were also consistent with that of the Atlantic silverside experiment (Conover and Munch, 2002). And the advance of sexual maturation and the increase in

reproductive investment supports the decrease in body size and weight of large-harvested populations (Enberg et al., 2012).

The changes in maturation and reproduction could affect population recruitment and recovery from overfishing (Stearns and Koella, 1986). Maturation and reproduction are important life history characteristics, significant for population supplementation. Size-selective harvesting has been shown to lead to earlier maturation (Allendorf and Hard, 2009; van Walraven et al., 2010; Sun et al., 2020). Our study also paralleled previous studies identifying earlier sexual differentiation and timing of the first spawning in large-compared to small- and random-harvested fish (Figs. 2, 3). In terms of causation, one proven postulation is that large-harvested populations allocate more energy into maturation instead of growth (Enberg et al., 2012; Reznick et al., 2000). Similarly, compared to large- and random-harvesting, the small-harvesting can induce organisms to allocate more energy to growth in the early life stage, leading to larger body sizes of populations at the same age (Fig. 7). However, the accelerated growth appears to help the populations quickly reach a body-size threshold, after which the energy flow to the reproduction increases. (Enberg et al., 2012; Heino and Kaitala, 1996). Therefore, the reduced energy flow to maturation is countered by the body size effect and does not necessarily delay the maturation (Fig. 2). Although the age at sexual differentiation and spawning were all earlier in large-harvested populations, the fecundity obviously decreased (Fig. 4). In order to adapt to large-harvesting, marine medaka showed earlier maturation and reproduction, which was the trade-off between reproduction and growth (Enberg et al., 2012; Jeschke and Kokko, 2009; Jørgensen et al., 2009). Based on our observations, earlier maturation definitively increases the probability of reproduction. However, the fecundity of small-sized fish is far lower than that of large fish (Fig. 4). Our result was consistent with previous research (Walsh et al., 2006). Additionally, the hatching rate was also significantly reduced while the larval mortality showed an increase (Figs. 5, 6). A possible factor may be the fitness costs of reproduction at a small body size (Walsh et al., 2006; Arlinghaus et al., 2010; Uusi-Heikkilä et al., 2010).

In our study, the hatching rate of the small-harvested populations was higher than that of the large-harvested populations. However, it was also lower than the random lines, which did not fit our projections (Fig. 5). One possible explanation was that the factors contributing to the reproductive advantage of small-harvesting populations were not quantifiably substantial to have an impact in this study, an impact possibly created due to lower harvesting pressure as compared to previous research (Walsh et al., 2006), and the similar ages at maturation and reproduction (Figs. 2, 3). Hence, the total reproduction energy of the small-harvested and random-harvested populations were at similar levels. In this case, when the small-harvested populations distributed more reproduction energy to the number of eggs, instead of the quality, only eggs possessing sufficient quality for healthy offspring could survive. In other words, the small-harvested populations would show a high fecundity, low hatching rate and a low larvae mortality at the same time (Figs.

4, 5, 6). Besides, compared to small body sizes, individuals with larger body sizes may have offspring with higher growth rates. It can help larval mortality decline (Hixon et al., 2014; Pepin, P, 1993; Rijnsdorp and Vingerhoed, 1994). However, fish with earlier maturation may increase the possibility of reproduction before fishing, but the offset is a higher larval mortality rate, thus reflecting a trade-off between offspring quality and age at maturity (Sinclair et al., 2002; Swain, 2011).

Effects of different harvesting times on marine medaka population traits

In general, harvesting after maturation could moderate the changes in phenotypes induced by size-selective harvesting. The average body size and weights of marine medaka harvested after maturation were smaller in the small-harvested populations, and larger in the large- harvested populations, than those harvested before (Figs. 7, 8). However, the differences between two kinds of harvesting times were nonsignificant. For the age at sexual differentiation and the first spawning, the changes of characteristics were similar and more obvious (Figs. 2, 3). Previous studies had shown that the medaka are at a low evolutionary limit for body size (Renneville et al., 2020), therefore, harvesting time had a significant effect on age at maturation but not on body size. Additionally, the fact that the harvesting time had non-significant effect on the eggs hatching rate also showed that compared to individuals themselves, harvesting time had a less impact on offspring (Fig. 5). When the fish are harvested at the immature life-history stages, fishing will select the fish with early maturation. It could conceivably induce stocks consisting of smaller and earlier mature individuals (Ernande et al., 2004; Hollins et al., 2018; Jorgensen et al., 2009). Furthermore, there were lower fecundity and higher larval mortality in populations harvested before maturation (Figs. 4, 6). The results conclusively showed immature individuals were more sensitive to fishing (Ernande et al., 2004).

In the study of different harvesting strategies, we found that small-harvesting could lead to larger body size and higher yield (Figs. 7, 8). And per our observations, pre-maturation harvesting might accelerate the changes. Perhaps in actual fishery production, this fishing method would make it possible to obtain greater yield in a short period. But in small-harvesting populations harvested before maturation, the age of maturation advanced in generation 4 (Fig. 2). Moreover, the fecundity was lower (Fig. 4) and larval mortality was higher (Fig. 6) than that of the populations harvested after maturation. It may be attributed to the earlier trade-off between growth and reproduction caused by pre-maturation harvesting. Due to the reduction of survival larvae, long- term fishing of immature fish may lead to an insufficient supplementary population, which could result in a diminished yield. Keeping the life history characteristics of fish in a slower pace of change is more conducive to long-term development. Harvesting mature fish using low fishing pressure could slow the change toward earlier maturation and provide more time for fish to grow (Ernande et al., 2004). It could serve as a reminder of the time of the closed season. The harvesting time should avoid the period before fish sexual maturation.

Harvesting and fishery management

Achieving sustainability in fisheries is a central goal in fisheries management (Dunlop et al., 2015). Many countries have adopted the closed season policy to protect economic species, such as Brazil and the Philippines (Macusi et al., 2021; Musiello-Fernandes et al., 2017). To protect fishery resources, there is also a closed season policy in China (Feng et al., 2019; Yan et al., 2019). However, the beginning time of the closed season should be reconsidered. Our results showed that the time of harvesting had an important effect on the biological traits of fish. Compared to harvesting before maturation, fishing after maturation could mitigate the effects of fishing pressure. The catching standard of aquatic animals should be based on the principle of reaching sexual maturity. However, the current closed season policy does not protect juveniles very well. It would be more beneficial to the conservation of fishery resources if the annual closed season could be flexibly adjusted according to the period for target species, which is determined by their life history characteristics. Moreover, the closed areas can be defined in more detail. Because one possibility of catching immature fish is that nursery and spawning areas are physically segregated, and harvesting operates in feeding areas (Ernande et al., 2004). Regulatory measures also impose a minimum size of fishing gear, which can protect the larvae from fishing. In China, the mesh regulation of major fishing gear, such as gill nets and purse seines, is set according to different sea areas and target species. Moreover, there are also some problems in small-selective harvesting, such as decreased hatching rates and earlier maturation. And in the actual fishing activities, fishing only for the small individuals could not produce a larger yield of fish, which is not conducive to the development of the fishery economy. Therefore, the existing fishery management system based on controlling minimum size restrictions should also be reconsidered. Adopting multiple fishing strategies for the target species may cause less evolutionary degradation.

Conclusively, this study suggests that size-selective fishing could induce rapid phenotypic changes in marine medaka. Selective harvesting of large individuals could lead to smaller body size, lower yield, earlier maturation, lower fecundity, lower hatching rate, and higher larval mortality. While selective harvesting of small individuals can increase body size, mean weight, fecundity and reduce larval mortality, after 4 generations, maturation occurs earlier, and the hatching rate of eggs decreases. Compared to harvesting before maturation, harvesting after maturation could mitigate some adverse changes. To protect fishery resources, we recommend that the closed season policy can be adapted to the life history characteristics of target species to protect immature fish. In addition, various fishing strategies could be adopted to slow down the evolution of target populations produced by fishing. This experiment also has some limitations. Our experiment did not consider the early life-history traits of marine medaka. In our future research, we will focus on the egg size, the larvae size, and the larvae growth rate. We will also measure length and weight at more ages to collect more data and calculate the growth rate. Also, we only focused on the impact of different fishing

strategies and times on marine medaka in this study. Yet, we acknowledge that in actual fishing activities, many uncontrolled variables such as climate change, habitat change, and interspecific competition can influence the life-history traits of fish. And since the need for a minimum-size limit size is to ensure that fish can reproduce at least once before being harvested, in further research, we may explore the effects of harvesting after the first spawning. Moreover, marine medaka have a short life history. Though the results are consistent with some life history characteristics of commercial fish species, organisms with different life cycles have different adaptabilities, which need further consideration.

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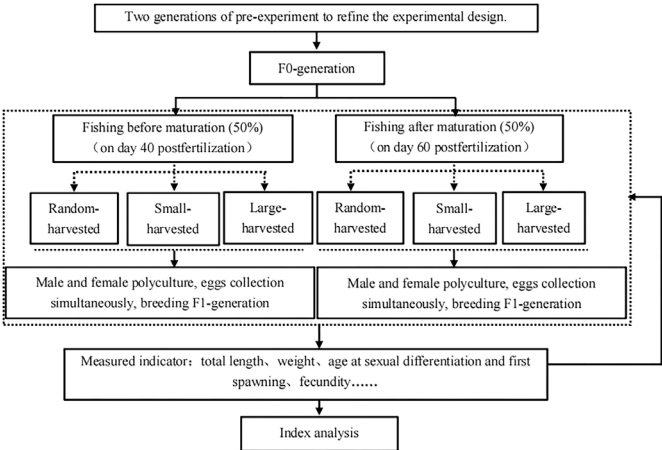
6. Figures

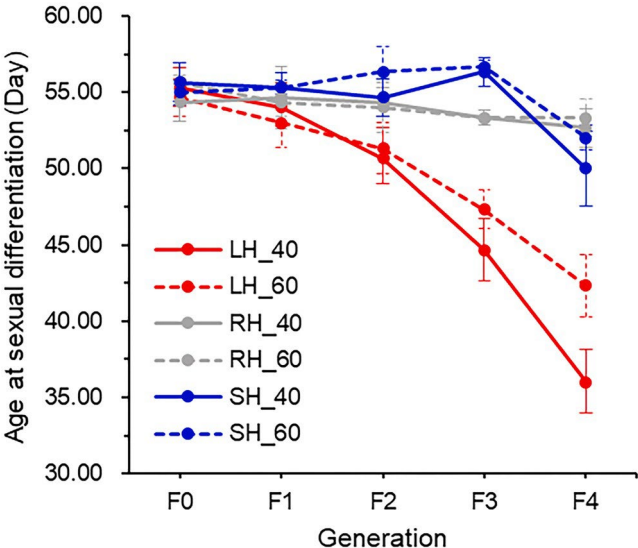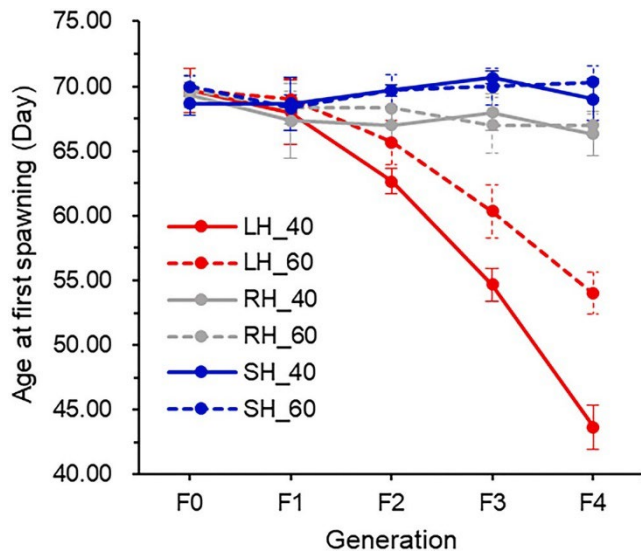Fig. 1. The setup of the size-selective harvest experiment.

Fig. 2. Trends in age at sexual differentiation across four generations of experimental harvest. Red lines represent the large-harvested (LH) populations. Blue lines represent the random-harvested (RH) populations and gray lines are the small-harvested (SH) populations. Dashed lines represent the populations harvested after maturation (Day 60), and the solid lines represent the populations harvested before maturation (Day 40). The vertical lines show the standard deviations.
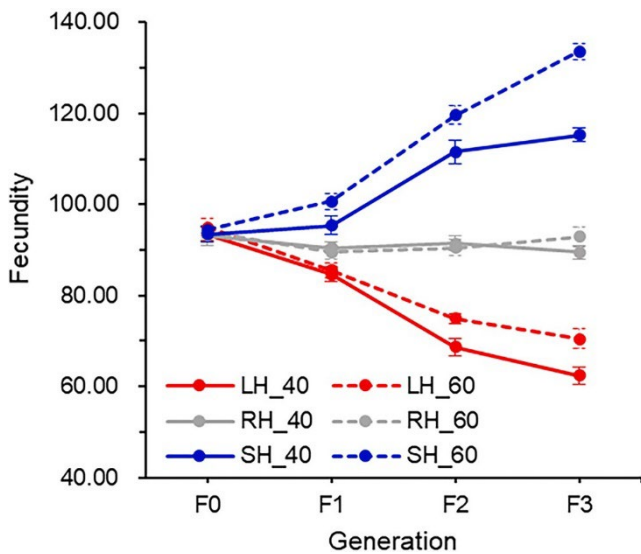
Fig. 3. Trends in age at first spawning across four generations of experimental harvest. Red lines represent the large-harvested (LH) populations, gray lines represent the random-harvested (RH) populations and blue lines are the small- harvested (SH) populations. Dashed lines represent the populations harvested after maturation (Day 60), and the solid lines represent the populations harvested before maturation (Day 40). The vertical lines show the standard deviations.

Fig. 4. Trends in fecundity across F0-F3 of experimental harvest. Red, gray, and blue lines are the large-, random- and small-harvested (LH, RH and SH) populations, respectively. Dashed lines represent the populations harvested after maturation (Day 60), and the solid lines are the populations harvested before maturation (Day 40). The vertical lines show the standard deviations.
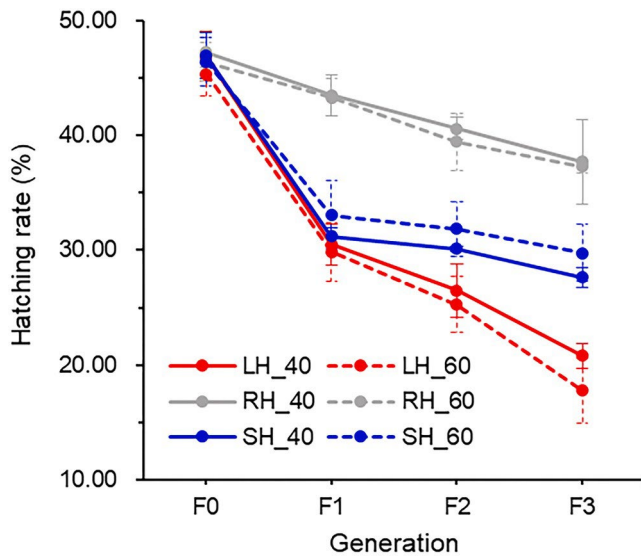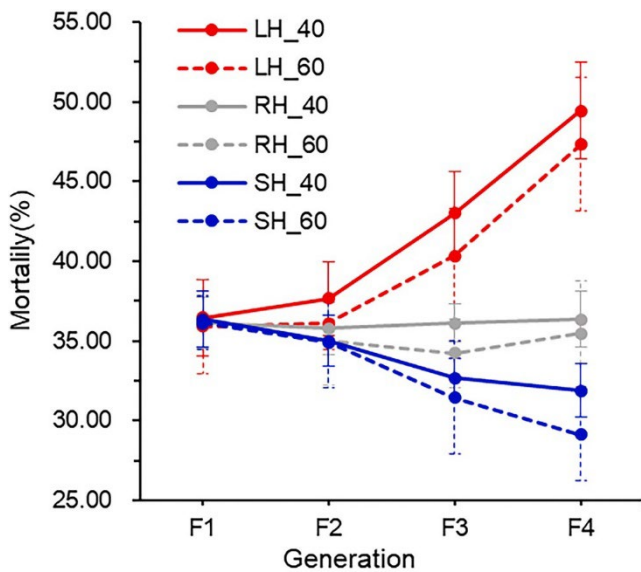
Fig. 5. Trends in hatching rate during F0-F3 of experimental harvest. Red, gray, and blue lines represent the large-, random- and small-harvested (LH, RH and SH) populations, respectively. Dashed lines represent the populations harvested after maturation (Day 60), and the solid lines are the populations harvested before maturation (Day 40). The vertical lines show the standard deviations.

Fig. 6. Trends in larval mortality across F1-F4 of experimental harvest. Red, gray, and blue lines are the large-, random-, and small-harvested (LH, RH and SH) populations, respectively. Dashed and solid lines represent the populations harvested after maturation and before maturation (Days 60 and 40). The ver- tical lines show the standard deviations.
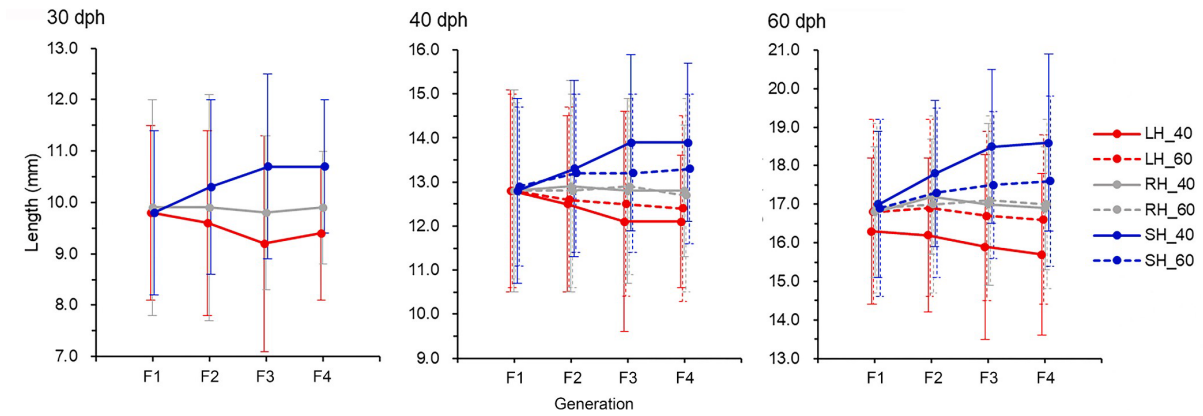
Fig. 7. Trends in lengths at the ages of 30, 40 and 60 dph across F1-F4 of experimental harvest. Red, gray, and blue lines are the large-, random-, and small-harvested (LH, RH and SH) populations, respectively. Dashed and solid lines represent the populations harvested after maturation and before maturation (Days 60 and 40). The vertical lines show the standard deviations.
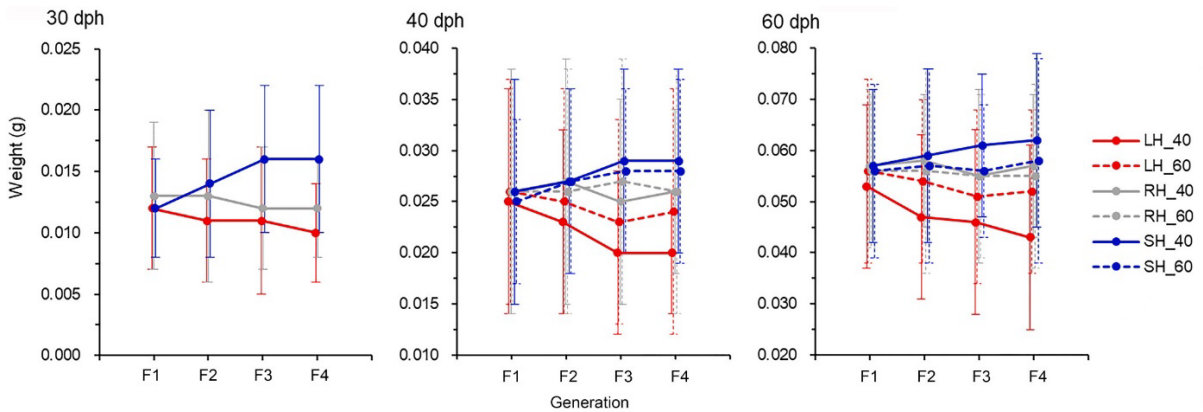

Fig. 8. Trends in weights at the ages of 30, 40 and 60 dph across F1-F4 of experimental harvest. Red, gray, and blue lines are the large-, random-, and small-harvested (LH, RH and SH) populations, respectively. Dashed and solid lines represent the populations harvested after maturation and before maturation (Days 60 and 40). The vertical lines show the standard deviations.