BIOLOGICAL SCIENCES

Density-dependent selection mediates harvest-induced evolution

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Abstract. Harvesting has been demonstrated to cause rapid, yield-decreasing trait change towards slower somatic growth and earlier maturation in wild populations. These changes are largely considered to result from direct, density-*in*dependent harvest selection on traits. Here, we show that exact same trait changes may also indirectly result from a harvest-induced relaxation of density-dependent (*K*) natural selection for faster growth and delayed maturation. We exposed 12 pond populations of medaka fish (*Oryzias latipes*) to contrasted size-selective harvesting during 5 years, and show that harvesting effectively changed juvenile natural mortality from density-dependent to density-*in*dependent. We then laboratory-reared medaka progeny under contrasted food levels mimicking the environmental effects of a harvest-induced density gradient. Interaction between past harvest regime and present food environment on progeny traits revealed that harvest-induced trait changes in medaka resulted from selection in a low-food environment only, i.e., were driven by relaxed *K*-selection only, not by direct harvest selection. Feeding trials further demonstrated that trait changes were associated with reorganizations in rates of food acquisition, assimilation and allocation that were contingent upon the food environments. This is the first study to demonstrate that harvesting can induce undesirable distortions of natural selection that impair productivity traits. We conclude that sustaining harvesting yields over extended time scales requires a preservation of high population densities.

Significance statement: Fisheries management often opposes a density-dependent approach which prioritize the preservation of high population densities, and an evolutionary approach which consider that alleviating change towards smaller body sizes is paramount to the sustainability of harvesting. The evolutionary approach consider harvest-induced body downsizing to be density-*in*dependent, i.e., to result only from direct harvest selection against large-bodied individuals. Here, we show instead that harvest-induced body downsizing may be density-dependent because, by decreasing population density, fishing relaxes natural, density-dependent selection for large-bodied individuals. Therefore, preserving population numbers and alleviating body downsizing in harvested populations are not independent lines of management, but are in fact two necessary and complementary routes to reaching the same management objectives.

Introduction

Harvesting potentially creates a mixture of selective pressures acting in parallel both directly and indirectly on life-history traits. In particular, size-selective harvesting directly selects against an old age, thus favoring early-maturing genotypes, and against large-bodied individuals at a given age, thus favoring slow-growing genotypes (1). This direct, “brute-force” warping of naturally-selected fitness landscapes is currently the prevailing model to explain harvest-induced evolution in wild populations (1–3). However, in parallel harvesting also lowers population densities and is thus susceptible to indirectly warp the naturally-selected fitness landscape through relaxing the strength of density-dependent natural selection (4), also known as *K*-selection (5–7). So far, however, this density-dependent pathway to harvest-induced selection remains unexplored empirically or experimentally. To bridge this gap in our knowledge, we conducted a 5-year size-selective harvesting experiment on 12 populations of medaka fish (*Oryzias latipes*) maintained in outdoor ponds under natural conditions with

no artificial feeding, followed by a 1-generation common garden experiment in the laboratory. The 12 founder medaka populations originated from parents wild-caught in Kiyosu (Japan).

In ponds, our experimental size-selective fishery removed 81% of the catch (catch rate = 98%) by specifically targeting large-sized individuals (Fig. 1a), and thus successfully reproduced a typical direct harvest selection pattern. In parallel, our experimental fishery relaxed negative density-dependence in medaka populations. Pond medaka populations followed Ricker stock-recruitment dynamics (Fig. 1b), a population dynamics model used in many fisheries management schemes (8). Fishing consistently decreased stock (population size in March) density below ca. 50 individuals (red squares in Fig. 1b), a density region in which increasing stock size had a positive effect on the number of summer-born juveniles (recruitment, black curves, Fig. 1b), indicating demographic “undercompensation” due to density-*in*dependence of vital rates (9). In contrast, unharvested populations had stock sizes above ca. 50 individuals (blue triangles in Fig. 1b), a density region where increasing stock size had a negative effect on recruitment, indicating demographic “overcompensation” due negative density-dependence of vital rates (black curves, Fig. 1b).

Overcompensating recruitment may operate through decreased fecundity and/or through increased mortality. To discriminate between the two mechanisms, we counted newborn larvae hiding in artificial vegetation in each pond during 3 years. In harvested populations, newborn medaka larvae were on average less numerous than in unharvested populations (P-value = 0.003, Fig. 2, Table S1), but average recruit numbers were similar among unharvested and harvested populations (85 vs. 73 recruits respectively, Fig. 1b, non statistically-significant difference), indicating that overcompensating recruitment was mediated by increased post-larval mortality in medaka populations.

Density-dependent post-larval mortality is expected to select for a larger body size and delayed reproductive investment. Experiments with *Drosophila* demonstrated that resource competition under a high density favors the evolution of increased food intake and/or conversion efficiency, ultimately resulting in faster somatic growth rates under standardized food conditions (10, 11). In fish, cannibalism is a further source of density-dependent mortality also predicted to favor faster somatic growth to larger body sizes (12, 13). Finally, high density and food limitation are expected to select for a delayed reproduction at a larger body size (6, 14, 15), a prediction that was validated in *Drosophila* (15). Therefore, we predicted that, exactly like direct harvest selection, harvest-induced relaxation of *K*-selection should have favored slower somatic growth rates and earlier maturation in medaka.

In a previous laboratory selection experiment, Kiyosu medaka were unable to respond to selection for a smaller body size but were able to respond to selection for a larger body size (16). This previous result suggests that any harvest-induced change in somatic growth or maturation evolved by pond medaka in the present experiment would more likely result from *K*-selection than from direct fishery selection. However, a further, efficient way to discriminate between the direct *vs*. density-mediated effects of harvesting is through the measurement of interactions between harvest treatments and food levels on trait expression (17–20). This is because the genes that control a given trait are often environment-specific (18–22). Consequently, trait differences measured under different standardized environments may be used to infer the direction of selection in each environment (17, 19, 20).

For instance, mice selected for a fast (slow) somatic growth in a high-food environment grow faster (slower) than unselected mice, but only in a high-food environment (18, 19). In contrast, mice selected

on somatic growth in a low-food environment showed a phenotypic response to selection under both a low- and high-food environments, suggesting that selection on somatic growth in a low-food environment tends to erase the sensitivity of growth to food variation (18–20). Following this rationale, we predicted that somatic growth response to direct, density-*in*dependent harvest selection in medaka should be manifest in a high-food environment, while somatic growth response to *K*-selection should be manifest in any food environment (19, 20).

Evolution of maturation is also expected to be contingent upon the food environment. For instance, predation-induced evolution towards earlier maturation in guppies *Poecilia reticulata* is more pronounced under a high-food environment because predators decrease guppy density and thus select in a high-food environment (17). Hence, we further predicted in medaka that maturation response to direct, density-*in*dependent harvest selection should be more pronounced in a high-food environment, while maturation response to *K*-selection should be more pronounced under a low-food environment (17).

Results

To test these predictions we measured in the laboratory the somatic growth of F_1 progeny from pond-sampled parents. We applied a low-, medium- and high-food regimes intended to mimic the environmental effects of an increasing harvest intensity from feeding the progeny once every second day to feeding twice daily.

Under all three food environments, harvested medaka grew significantly slower than unharvested medaka (low food P-value = 0.008, medium food P-value < 0.001, high food P-value = 0.002, Fig. 3a).

Accordingly, a deviance analysis shows that there was no significant harvest by food interaction (P-value = 0.2650, Table 1), indicating that the amplitude of harvest-induced decrease in somatic growth was food-independent. This result suggests that medaka responded to selection for fast-growth in a low-food environment (19, 20), i.e., responded to *K*-selection for faster somatic growth, but not to direct harvest selection for slower somatic growth in a high-food environment. This result is further in line with our previous finding that medaka from Kiyosu are unable to respond to selection for slower somatic growth under laboratory conditions but that they do respond to selection for faster somatic growth (see above).

Supporting our second prediction, a deviance analysis shows that the effect of harvesting on the age-dependency of maturation was significantly food-dependent (Age × Harvesting × Food interaction, Table 1). Specifically, harvesting changed the size-corrected effect of age on maturation probability from significantly positive (P-value = 0.025, Table S1) to significantly negative (P-value = 0.020, Table S1), reflecting that harvesting induced earlier maturation only in a low-food environment (Fig. 3b). These results suggest that medaka responded to selection for delayed maturation in a low-food environment (17), i.e., responded to *K*-selection, but not to direct harvest selection for earlier maturation in a high-food environment. In line with this result, we previously found that Kiyosu medaka are unable to respond to selection for earlier maturation in the laboratory (16).

K-selected changes in somatic growth and maturation may be mediated by combined changes in energy acquisition, assimilation or allocation rates. To gain insights into these regulatory pathways we measured acquisition rates through individual feeding trials on laboratory-born F_1 individuals. We

starved fish overnight, presented them with 20 prey (nauplii of *Artemia salina*), and counted the number of prey eaten during 5 minutes (repeated 3 times per individual).

Progeny from harvested populations ate significantly less prey than progeny from unharvested populations, but only in a medium-food environment (P-value = 0.011, Fig. 3c). This result suggest that changes occurred in all three pathways of energy acquisition, assimilation and allocation, but that the respective contributions of these pathways to the expression of life-history change was environment-specific. In a low-food environment, slower somatic growth (Fig. 3a), earlier maturation (Fig. 3b) but unchanged energy acquisition (Fig. 3c, P-value = 0.523) in harvested medaka together suggest energy re-allocation from growth to reproduction. In a medium-food environment, the slower somatic growth (Fig. 3a) of in harvested medaka was apparently mediated by decreased energy acquisition (Fig. 3c), but unchanged maturation (Fig. 3b) also suggests energy re-allocation from growth to reproduction. Finally in a high-food environment, slower somatic growth (Fig. 3a) but unchanged rates of maturation (Fig. 3b) and energy acquisition (Fig. 3c, P-value = 0.424) together suggest decreased energy assimilation rates in harvested medaka. These results are consistent with previous studies showing that evolution towards slower somatic growth in fish may be underlaid by decreases in food consumption rate and conversion efficiency (23).

Discussion

Our results demonstrate that harvesting caused evolution towards slower somatic growth and earlier maturation in medaka through relaxed *K*-selection. However, in ponds the body size of 0+ juvenile medaka did not show any statistically significant temporal trend in harvested or unharvested populations (MCMC P-values = 0.365 and 0.262, respectively, Fig. 4). Phenotypic stasis despite known

evolutionary change (i.e., cryptic evolution) is typical of responses to environmental deterioration where decreased environment quality selects for higher competitive ability but, as highly competitive genotypes spread in the population the environment further deteriorates, resulting in no detectable effects on phenotypes (24, 25). Such cryptic “Red Queen” evolutionary dynamics are expected in all density-dependent populations and are thus probably commonplace in harvested systems. However, their detection requires using common garden experiments or specific quantitative genetic methods (24, 25), and studies of harvest-induced trait change based on field data published so far thus maybe underestimate potential for harvest-induced evolution.

The direct and density-dependent pathways to harvest-induced selection act in the same direction on life-history traits, but have different implications for management. Phenotypic changes from direct harvest selection may be alleviated by moulding the shape of artificial selection onto the shape of natural selection through, for instance, adjusting gear selectivity. In contrast, the consequences of density-dependent harvest selection can be alleviated only by relaxing the harvest effort (4). Additionally, post-moratorium phenotypic recovery from direct harvest selection is expectedly slow because the strength of natural selection is predicted to be constant and modest relative to the strength of harvest selection. In contrast, recovery from density-dependent harvest selection should be rapid because natural selection strengthens when fishing is relaxed (13).

Recent studies have shown that predator-induced life-history evolution may be, at least partly, mediated by relaxed *K*-selection (26) and by an associated adaptation to increased food availability (17). Our study reinforces and extends these previous results by experimentally demonstrating that harvest-induced trait changes previously ascribed to direct, density-independent selection in the literature may,

in fact, have also emerged through a relaxation of *K*-selection. Hence, the more ecologically sustainable harvesting strategies also produce smaller evolutionary changes (4), and the next-generation harvest management methods should thus converge towards an integration of the reciprocal effects between ecological dynamics and rapid evolutionary change.

Materials and Methods

Pond medaka populations

Origin and maintenance

Our start medaka populations descended from 100 wild medaka caught in Kiyosu (27) (Toyohashi, Aichi Prefecture, Japan) in June 2011. These 100 Japanese breeders were maintained in five 20L aquariums and their eggs were collected daily from July to September 2011. Hatched larvae were stocked in 12 circular outdoor ponds (3.57 m diameter, 1.2 m deep).

Prior to medaka introduction, the 12 ponds were bottom-coated with a 5 cm layer of Loire River sand, filled with tap water and mildly enriched with a plant fertilizer. After a few weeks of algal development, tanks were seeded with a diverse community of zooplankton collected from surrounding water bodies. Medaka introduction was performed after ponds had reached a clear-water state indicating algal control by zooplankton. After introduction, two pairs of floating plastic brushes were placed in each tank to provide fish with a spawning substrate and shelter for larvae. Each pond was covered with a net to prevent avian predation, and was outlet-secured with a stainless steel filter to prevent any fish or egg escapement. No food was added to the ponds which thus represented natural, replicated ecosystems.

Medaka harvesting and phenotyping in ponds

From 2012 to 2016, each of the 12 pond populations was sampled in March before medaka reproduction (pre-recruitment) and in November after medaka reproduction (post-recruitment). Fish were concentrated using a seine net and then fished using handnets (catchability = 98 ± 0.6% SD estimated using removal sampling). All sampled fish were individually weighted to the nearest mg and estimated for standard body length (from the tip of the snout to the base of the caudal fin) using a body mass-length relationship (R^2 = 0.98 on a log-log scale, n = 2722). In March in the 6 harvested populations all the fish that were too large to pass through a 2 mm-wide screen were removed, while in unharvested populations all fish were released after phenotyping. In November, all fish from both harvested and unharvested populations were released after phenotyping.

Larvae counts

We visually counted the number of newly-hatched larvae hiding in each pair of floating plastic brushes (summed for the two brush pairs) from one to three times per day at irregular intervals during the 2014, 2015 and 2016 spawning periods (April to September).

Medaka F_1 in the laboratory

Parental fish

In November 2016, between 6 and 10 individuals were randomly kept from each of the 12 pond populations to serve as parents for a F_1 generation in the laboratory. These parental fish were maintained in a greenhouse at air temperature in 12, 150L tanks with live food. In January 2017, parental fish were weighted to the nearest mg, measured for standard body length with ImageJ, and grouped to form 3 breeding pairs per population (except one harvested population that had only one

female). Each of the resultant 36 pairs was transferred to the laboratory in a 3.5L aquarium and induced to spawn by progressively raising temperature to 27.0 ± 0.3°C and setting a 15-h light:9h dark photoperiod. Dry food (Skretting Gemma Micro) was provided twice per day and live nauplii of *Artemia salina* once per day. After initiation of spawning by all breeding pairs, eggs from each breeding pair were collected daily during a 4-day period, enumerated and incubated in separate jars so as to keep track of individual parental identity (but not spawning day). We found no significant effect of the harvest treatment on parental body size, body condition, fertility or fecundity.

F_1 progeny phenotyping and food environments

We collected F_1 larvae born from the 7th to the 10th day after the weighted average date of spawning. Larvae hatched from the same breeding pair on the same day were transferred to 1.5L aquariums by groups of 3 larvae, and were maintained under the same temperature and light regime as their parents. We kept 1-4 groups of F_1 larvae per breeding pair (average 2.9 groups per breeding pair). At 15 days post hatch (dph), all F_1 individuals were weighted and measured as described above and only one individual per aquarium was randomly kept for subsequent phenotyping, making it possible to track individual developmental trajectories. Individual phenotyping was repeated at 30 dph, 40 dph and then once per week until 90 dph (11 individual measurements). From 40 dph onwards, phenotyping further included detection of the maturity status from the presence of secondary sexual characters (28). Specifically, the maturity criteria were first appearance of a round-shaped anal papilla in females, and of the papillar process on the anal fin in males. Additionally, at around 48, 56 and 63 dph, each individual F_1 medaka was measured for feeding rate. We counted the number of live prey (nauplii of *Artemia salina*) eaten when the medaka was placed alone with 20 prey during 5 minutes in a 80 mL container. Medaka were starved overnight prior to each behavioural test.

From 15 dph onwards, we varied resource levels by applying three food environments to F_1 progeny. We chose feeding regimes so has to mimic a high-density, scarce-food environment in which predators are not able to daily catch a prey, a low-density, food-rich environment in which predators are replete with prey, and an intermediate environment. In the low-food environment, individuals were fed with 2mL of a solution containing nauplii of *Artemia salina* at a standard concentration on day 1, nothing on day 2, dry food (see below) on day 3, nothing on day 4 and so on. In the high-food environment, medaka were fed twice daily, once with nauplii and once with dry food. Finally, in the medium-food environment, medaka were fed once daily alternating nauplii and dry food.

Volume of dry food doses and pellet size were increased during fish development to fit with the ontogenetic increase in energy needs and prey size. From 0 to 40 dph, 40 to 60 dph, and 60 dph onwards, medaka received daily 4, 6 and 14µL of food, respectively. From 0 to 20 dph, 20 to 40 dph, and 40 dph onwards, dry food was made from 100% 150 µm pellets, 50% mixture of 150-300 µm pellets and 100% 300 µm pellets, respectively.

Statistical analyses

We below provide a short summary of the statistical analyses. A full description is given in the SI Appendix.

Analysis of pond data

Medaka age was inferred by fitting a mixture of two Gaussian distributions to individual standard body lengths measurements (n = 17908). We further estimated temporal trends in body size of November 0+ recruits (n = 9688 individuals) using a version of the Gaussian mixture model that was modified to include a harvest treatment-specific (n = 2 treatments) hierarchical regression of mean recruit standard body length on year of sampling (n = 5 years). We estimated the relationship between individual standard body length and probability to survive through the fishery in March (n = 3970 individuals) using a mixed effects Bernoulli GLM with a logit link function. The Gaussian mixture model described above allowed us to estimate the number of November 0+ recruits in each pond and year. We then visualized the strength of negative density-dependence in pond medaka populations by plotting Ricker "stock-recruitment" relationships (Fig. 1b). Finally, larvae counts in ponds were modelled using a mixed-effects zero-inflated negative binomial model, which parameter estimates are provided in Table S1.

Analysis of laboratory data

We estimated the effects of harvesting and food environments on the growth trajectories of F_1 progeny in the laboratory using a second order polynomial regression of standard body length on age (parameter estimates provided in Table S1). We fitted probabilistic maturation reaction norms (PMRNs) to medaka maturation data using the "direct estimation" method for PMRNs (29) in a mixed-effects Bernoulli GLM with a logit link function (parameter estimates provided in Table S1). Counts of the number of nauplii larvae eaten by individual medaka were modelled using a mixed-effects zero-inflated negative binomial model (parameter estimates provided in Table S1).

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Author contributions. ABH performed the laboratory F_1 experiment, contributed to data analysis, wrote the first draft of the manuscript and contributed to subsequent versions. EE designed the study, contributed to the pond experiment, performed data analysis, and led manuscript writing from the second version. JM, DC, SA, AM, SP, EM and BD contributed to the pond and laboratory experiments.

Competing interests. The authors declare no competing interests.

Data archiving statement. All data and codes used in this paper will be archived.

Ethical statement. The protocols used in this study were designed to minimize discomfort, distress and pain of animals, and were approved by the Darwin Ethical committee (case file #Ce5/2010/041).

Supplementary Materials

Table S1: MCMC parameter estimates for models 4-7.

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Table 1. Analysis of deviance table for GLMs testing for the harvest by food interaction on life-history traits in laboratory-born F_1 medaka progeny. The "Deviance" column gives the reduction in the residual deviance as each predictor is added in turn into the model. The P-values compare the reduction in deviance to the residual deviance in an F test.

Trait	Distribution	Link	Predictor	Df	Deviance	Resid. DF	Resid. Dev	F	P-val
Body length	Gaussian	Identity	Age	1	18100	1130	2651	17144	**<0.0001**
			Age^2	1	468	1129	2183	443	**<0.0001**
			Harvesting	1	130	1128	2053	123	**<0.0001**
			Age x Harvesting	1	24	1127	2029	22	**<0.0001**
			Age x Food	2	841	1125	1188	398	**<0.0001**
			Age x Harvesting x Food	2	3	1123	1186	1	0.2650
Maturation	Bernoulli	Logit	Age*	1	96	589	432	164	**<0.0001**
			Length*	1	97	588	335	166	**<0.0001**
			Harvesting	1	2	587	333	3	0.064
			Food	2	3	585	329	3	0.0513
			Age* x Harvesting	1	8	584	321	14	**0.0002**
			Length* x Harvesting	1	1	583	320	2	0.1745
			Age* x Food	2	12	581	309	10	**<0.0001**
			Length* x Food	2	1	579	307	1	0.3263
			Age* x Harvesting x Food	2	10	577	297	9	**0.0002**
			Length* x Harvesting x Food	2	2	575	295	2	0.2027

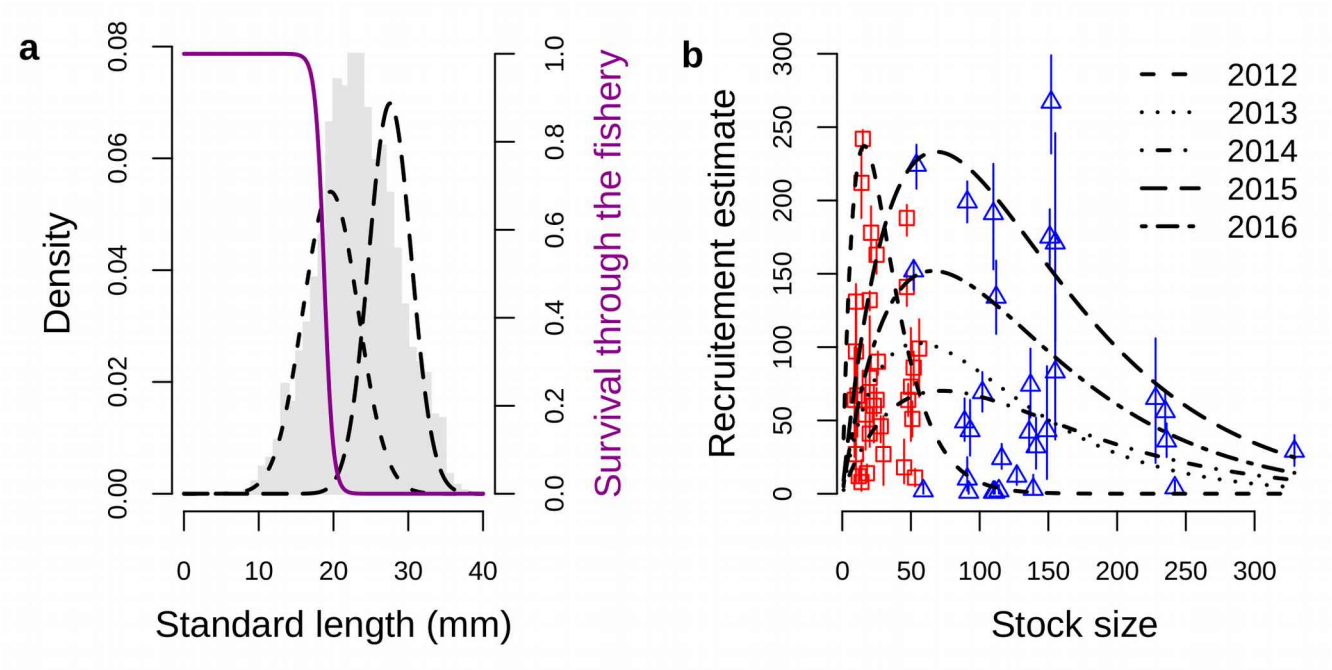

Fig. 1. Direct and density-mediated harvest-selection in ponds. a: Size- and age-dependent harvest selection. Light grey bars represent raw standard length data in harvested populations. Superimposed Gaussians represent mean MCMC estimates for the density of 0+ juveniles (short-dashed curve) and 1+ and older adults (long-dashed curve) individuals. The magenta logistic curve shows the mean relationship between exploitation rate by the fishery and standard body length. **b: Stock-recruitment relationships.** Points show mean MCMC recruitment estimates with 95% credible intervals for unharvested (blue triangles) and harvested (red squares) populations. Black curves show year-specific Ricker functions fitted to mean estimates using maximum likelihood.

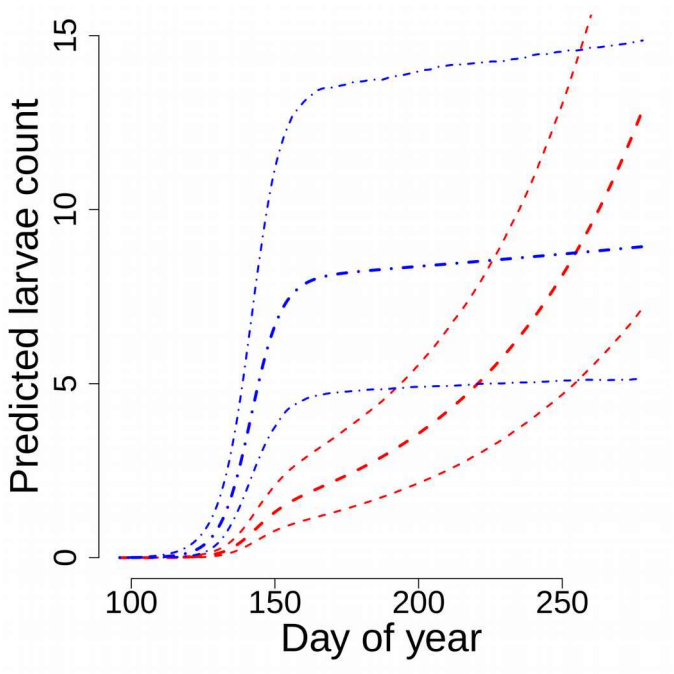

Fig.2. Larvae count seasonal dynamics in ponds. Thick curves represent mean MCMC estimates for daily counts of newly-hatched larvae for unharvested (dot-dashed, blue curve) and harvested (dashed, red curve) populations. Thin curves show 95% credible intervals around mean MCMC estimates.

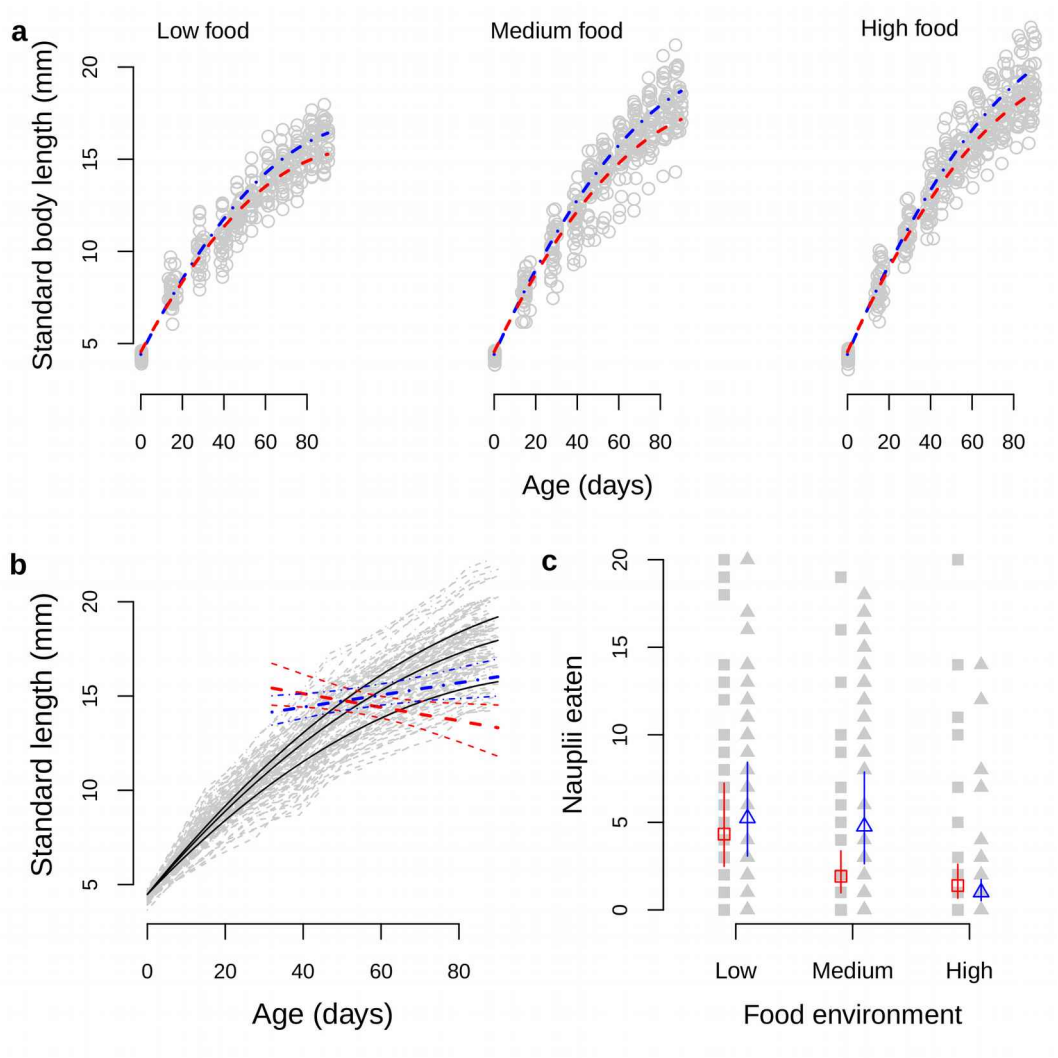

Fig. 3. Individually-raised F_1 progeny in the laboratory. a: Mean growth trajectories. MCMC mean growth curves for individuals originating from unharvested (dot-dashed blue curves) and harvested (dashed red curves) populations in a low-, medium- or high-food environments. Grey dots show the raw data. **b: Probabilistic maturation reaction norms (PMRNs).** PMRNs show the combination of age and lengths at which maturation probability equals 0.5. They account for the plastic effect of growth on maturation, and a shift in PMRNs is thus suggestive of a non-plastic, evolutionary change in maturation schedules (30, 31). Coloured lines show MCMC mean estimates with 95%

credible intervals for PMRNs of medaka originating from unharvested (dot-dashed blue line) and harvested (dashed red line) populations. Thin grey curves in the background show raw growth trajectories for medaka originating from unharvested (dot-dashed) and harvested (dashed) populations. Solid black lines show the mean growth trajectories in a low-, medium- or high-food environment (averaged across harvesting treatments). **c: Feeding rates.** Coloured, open points symbols show mean MCMC estimates with 95% credible intervals for the number of prey eaten by medaka originating from unharvested control (blue triangles) and harvested (red squares) populations and maintained in a low-, medium- or high- food environment. Grey, filled symbols show the raw data.

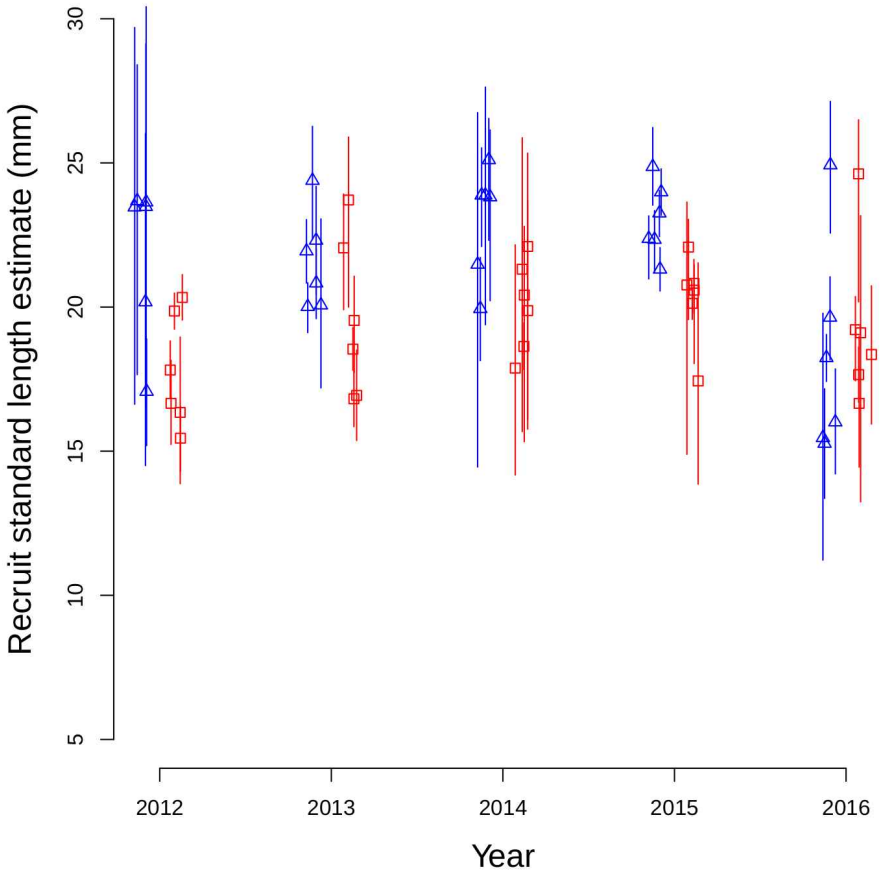

Fig. 4. Body length time series estimates for November 0+ recruits in pond medaka populations. Points show mean MCMC recruitment estimates with 95% credible intervals for unharvested (blue triangles) and harvested (red squares) populations.

Supplementary Information for

Density-dependent selection mediates harvest-induced evolution

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This PDF file includes:

Supplementary methods: statistical analyses.

Table S1.

Statistical analyses

Medaka aging in ponds

Medaka juveniles are too small to be tagged and, unlike in Japan (*1*, *2*), no winter check was deposited in medaka otoliths in our experimental populations. We therefore relied on analysis of length-frequency distributions to infer medaka age. We fitted a mixture of two Gaussian distributions to individual standard body lengths Sdl_i :

$$\begin{aligned} &Sdl_i \sim \sum_{j=1}^{J}\sum_{k=1}^{K} \pi_{j,k} N\left(\mu_{j,k}, \sigma_j^2\right) \\ &\mu_{2,k} \sim N\left(\mu_{H[k]}, \sigma^2\right) \\ &\mu_{1,k} = \delta_k \mu_{2,k} \\ &\delta_k \sim U(0,1) \end{aligned} \quad (1a),$$

where i indexes individuals (n = 17908), j indexes age groups (0+ *vs*. 1+ and older such that $J = 2$), k indexes a sampling event, i.e., indexes one population in a particular year and month ($K = 109$ sampling events), N is the normal distribution, and U is the uniform distribution. $H[k]$ indexes the harvest treatment (harvested *vs*. non harvested) associated with sampling event k. $\pi_{j,k}$ is the proportion of age j individuals at each sampling event k such as for each k:

$$\pi_j \geq 0, \sum_{j=1}^{J} \pi_j = 1 \qquad \text{(1b).}$$

Indexes in line 1 in Eq. 1a show that our model estimated a mean standard body length separately for each age group at each sampling event, while body length variance was assumed to vary only with age. Line 2 in Eq. 1a shows that we assumed the mean standard body length of age 1+ and older medaka at each sampling event $\mu_{2,k}$ to be a normally-distributed random variable with mean specific to each harvest treatment, because harvesting was expected to restrict the maximum age and size of medaka. Lines 3-4 in Eq. 1a show that mean standard body length of 0+ medaka at each sampling event $\mu_{1,k}$ was estimated as proportional to $\mu_{2,k}$ with a proportionality constant δ_k following a uniform distribution U between 0 and 1. Model 1 provided us with MCMC age samples for each individual fish in the dataset, allowing us to compute age-specific survival rates through the fishery.

We estimated temporal trends in mean standard body length of November 0+ recruits using a modified version of model 1 that included a hierarchical regression:

$$
\begin{aligned}
&Sdl_i \sim \sum_{j=1}^{J}\sum_{k=1}^{K} \pi_{j,k} N\left(\mu_{j,k}, \sigma_j^2\right) \\
&\mu_{2,k} \sim N\left(\mu_{H[k]}, \sigma_2{}^2\right) \\
&\mu_{1,k} \sim N\left(\hat{\mu}_{1,k}, \sigma_1{}^2\right) \\
&\hat{\mu}_{1,k} = \alpha_{H[k]} + \beta_{H[k]} Year_k
\end{aligned}
\qquad (1c)
$$

where i indexes November-sampled fish (n = 9688 individuals, K = 60), $\alpha_{H[k]}$ and $\beta_{H[k]}$ are harvest treatment-specific temporal regression parameters, and $Year$ was scaled to 0 mean. Other variables and subscripts are as described above.

Fishery exploitation rate and selection in ponds

We estimated the relationship between individual standard body length and probability to survive through the fishery using a Bernoulli GLM with a logit link function:

$$
\begin{aligned}
&y_i \sim Bern\left(p_i\right) \\
&\ln\left(\frac{p_i}{1-pi}\right) = \alpha_0 + \alpha_{j[i]} + \left(\beta_0 + \beta_{j[i]}\right) Sdl_i \\
&\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_\alpha & \rho\,\sigma_\alpha \sigma_\beta \\ \rho\,\sigma_\beta \sigma_\alpha & \sigma_\beta \end{pmatrix}\right)
\end{aligned}
\qquad (2),
$$

where subscripts i and j index individuals (n = 3970) and groups, respectively, to which individuals belong. There was n = 6 fished populations and n = 5 sampling years, yielding $j = 1,2\ldots30$ groups. Finally, $Bern$ is the Bernoulli distribution, and $\ln$ is the natural logarithm.

Eq. 2 indicates that we modelled the intercept and slope of the survival-mass relationship as normally-varying among groups j, including a correlation parameter ρ between intercept and slope.

Parameter estimates α_0 and β_0 from Eq. 2 define a mean size-dependent survival function $s(Sdl)=1/(1+\exp(-(\alpha_0+\beta_0 Sdl)))$ plotted in Fig. 1a.

Stock-recruitment relationship in ponds

Model (1) described above allowed us to estimate the number R_k of 0+ medaka (recruits) at each November sampling event k (n = 60 November sampling events). We then visualized the strength of negative density-dependence in pond medaka populations by plotting (Fig. 1b) Ricker (*3*) "stock-recruitment" relationships between R_k and the number S_k of fish released in March (stock of spawners):

$$\begin{gathered} R_k \sim P(\lambda_k) \\ \ln(\lambda_k)=\ln(S_k)+\alpha_{Year[k]}+\beta_{Year[k]} S_k \end{gathered} \quad (3),$$

where P is the Poisson distribution and $Year[k]$ indexes indicate that one Ricker curve was fitted for each year from 2012 to 2016.

Larvae counts

Larvae counts L followed a zero-inflated negative binomial distribution and were modelled as (*4*):

$$\begin{aligned} & L_i \sim NB(\phi_i, r_i) \\ & \phi_i=\frac{r_i}{r_i+\lambda_i(1-\theta_i)} \\ & r_i=\gamma_{H[i]} \\ & \ln(\lambda_i)=\alpha_{Year[i],Pond[i]}+\beta_{H[i]}+\delta_{H[i]} Day_i \\ & \alpha_{Year[i],Pond[i]} \sim N(0,\sigma_\alpha^2) \end{aligned} \quad (4a),$$

where subscript i indexes sampling events corresponding to a given observer in a given pond on a given sampling day (n = 2,004 sampling events), NB is the negative binomial distribution with success probability ϕ and number of failures r. Lines 4 and 5 in Eq. (4a) show that we modelled positive (non-zero) counts λ as harvest treatment-specific linear regressions of the day of year (scaled to 0 mean), with a normally-distributed random effect of the year and pond combination (n = 36 groups).

The θ latent variable for absence of larvae was modelled as a Bernoulli process having a linear dependency on the day of year:

$$\theta_i \sim B(\psi_i)$$
$$\ln\left(\frac{\psi_i}{1-\psi_i}\right) = \zeta + \omega\, Day_i \quad \text{(4b)},$$

where B is the Bernoulli distribution with probability for absence of larvae ψ.

Line 3 in Eq. 4A shows that we allowed for r, which enters in the computation of the variance of the distribution (*4*), to be different among the two harvest treatments H. Harvest treatment-specific mean larvae count is given by $E(L_H) = \bar{\lambda}_H(1-\bar{\theta})$ and variance by $var(L_H) = \bar{\lambda}_H(1-\bar{\theta})(\bar{\lambda}_H(1-\bar{\theta}) + \gamma_H)$, and we computed the dispersion index (*4*) in each harvest treatment as $DI_H = E(L_H)/var(L_H)$ (Table S1).

Somatic growth trajectories of F_1 progeny in the laboratory

We estimated the effects of harvesting and food environments on medaka growth trajectories using a second order polynomial regression of standard body length on age:

$$\begin{gathered} Sdl_i \sim N\left(\mu_i, \sigma_i^2\right) \\ \mu_i = \alpha_{P[i]} + \beta_{H[i]} + \left(\gamma_{H[i],F[i]} + \delta_{P[i]}\right) * Age_i + \eta\, Age_i^2 \\ \alpha_{P[i]} \sim N\left(0, \sigma_\alpha^2\right) \\ \delta_{P[i]} \sim N\left(0, \sigma_\delta^2\right) \\ \ln\left(\sigma_i^2\right) = \mathrm{A}_{H[i],F[i]} + \mathrm{B}_{H[i],F[i]}\, Age_i \end{gathered} \qquad (5),$$

where i indexes observations (n = 1144 observations from 104 individuals), $H[i]$ indexes the harvest treatment associated with observation i, $H[i], F[i]$ indexes the interaction of harvest treatment and food environment (n = 2 * 3 = 6 groups), and $P[i]$ indexes the parental breeding pair associated with observation i (n = 36 pairs), treated as a normally-distributed random effect on both size-at-hatch α and linear somatic growth rate δ (lines 3 and 4 in Eq. 5, respectively).

In this model, we assumed both linear somatic growth rate and the regression of (ln-transformed) residuals variance on age to be different among harvest treatments and food environments (lines 2 and 5 in Eq. 5, respectively). In contrast, size-at-hatch $\beta_{H[i]}$ was allowed to vary only due to harvest treatment because food environments were applied only starting from 15 dph.

Probabilistic maturation reaction norms of F_1 progeny in the laboratory

Probabilistic maturation reaction norms (PMRNs) describe the probability that an immature individual at a given age and size will mature during a given interval of time (*5*). Provided that plasticity in the maturation process is captured by growth trajectories, PMRNs separate the effects of evolution from

plasticity on maturation. PMRNs have been extensively used to explore genetic effects of exploitation on the maturation process in wild populations (*6*, *7*). Following the "direct estimation" method for PMRNs (*7*), we fitted a Bernouilli model to individual medaka maturity (0 or 1) data y_i, truncated so as to keep only the first maturity event for each individual:

$$\begin{gathered} y_i \sim B(\mathrm{M}_i) \\ \ln\left(\frac{\mathrm{M}_i}{1-\mathrm{M}_i}\right) = \alpha_{P[i]} + \beta_{H[i]} + \gamma_{H[i]} Age_i + \delta_{H[i]} Sdl_i \\ \alpha_{P[i]} \sim N(0, \sigma_\alpha^2) \end{gathered} \qquad (6),$$

where M is maturity probability. Other subscripts or variables are as described above. Eq. 6 shows that we allowed harvest-specific intercept and slopes of age and standard body length effects on maturation probability. Harvest-specific PMRNs corresponding to length at 50% maturation probability for each age in each treatment group H was then computed as $Sdl50_H = -(\beta_H + \gamma_H Age)/\delta_H$.

Predatory behaviour of F_1 progeny in the laboratory

Counts C_i of number of prey eaten by individual medaka followed a zero-inflated negative binomial distribution and were modelled similarly as larvae counts in model 4 above:

$$\begin{aligned} & C_i \sim NB(\phi_i, r_i) \\ & \phi_i = \frac{r_i}{r_i + \lambda_i(1-\theta_i)} \\ & r_i = \gamma_{H[i],F[i]} \\ & \ln(\lambda_i) = \alpha_{I[i]} + \beta_{H[i],F[i]} \\ & \alpha_{I[i]} \sim N(0, \sigma_\alpha^2) \end{aligned} \qquad (7a),$$

where number of failures r and positive (non-zero) counts λ were both modelled as being different among harvest treatments H in each food environment F, while $\alpha_{I[i]}$ was a normally-distributed random individual effect on λ (n = 3 counts per individual). The θ latent variable was modelled as:

$$\begin{gathered}\theta_i \sim B(\psi_i) \\ \ln\left(\frac{\psi_i}{1-\psi_i}\right) = \gamma + \delta_{I[i]} \\ \delta_{I[i]} \sim N(0, \sigma_\delta^2)\end{gathered} \quad \text{(7b)},$$

where δ_I is a normally-distributed random individual effect.

Analysis of deviance

We tested for the overall statistical significance of harvest by food interaction on somatic growth and maturation in the laboratory using analyses of deviance. Specifically, we fitted the following models:

$$\begin{gathered}Sdl_i \sim N(\mu_i, \sigma_i^2) \\ \mu_i = \alpha_{H[i]} + (\beta_{H[i]} + \gamma_{F[i]} + \delta_{H[i],F[i]}) Age_i + \zeta Age_i^2\end{gathered} \quad \text{(8), and}$$

$$\begin{gathered}y_i \sim B(\mathrm{M}_i) \\ \ln\left(\frac{\mathrm{M}_i}{1-\mathrm{M}_i}\right) = \alpha_{H[i]} + \beta_{F[i]} + (\gamma_{H[i]} + \delta_{F[i]} + \zeta_{H[i],F[i]}) Age_i + (\eta_{H[i]} + \theta_{F[i]} + \iota_{H[i],F[i]}) Sdl_i\end{gathered} \quad \text{(9)},$$

where variables are as in models (5) and (6). We then used an F test to evaluate the significance of each predictor separately (Table 1).

Parameter estimation

Models 3, 8 and 9 were fitted using maximum likelihood (glm function) in R 3.4.4 (*8*). Other models were fitted by Markov chain Monte Carlo (MCMC) in JAGS 4.2.0 (*9*), through the jagsUI package (*10*). To ease model convergence and avoid slope-intercept correlations, all numerical predictors were scaled to zero mean. For each model, we ran three independent MCMC chains thinned at a period of 5 iterations until parameter convergence was reached, as assessed using the Gelman–Rubin statistic (*11*).

Parameter estimates for models 4-7 are provided in Table S1. Statistical significance of harvest- and food-treatment effects reported in the main text was assessed from the posterior distributions of parameter differences in a test equivalent to a bilateral *t* test. In these tests, the MCMC P-value was twice the proportion of the posterior for which the sign was opposite to that of the mean posterior value. For instance, in Eq. 4a the posterior differences $\beta_{H=1}-\beta_{H=0}$ and $\delta_{H=1}-\delta_{H=0}$ measure the effect of harvest treatment (H = 0 for unharvested, H = 1 for harvested) on intercept and slope of day effect for $\ln(\lambda)$, respectively.

Priors were chosen to be weakly informative. In model 1 we used a Dirichlet prior for the $\pi_{j,k}$ and prevented label switching by assigning age class 0+ to fish shorter than 8 mm and age class 1+ and older to fish longer than 35 mm (*12*).

We assessed goodness of fit of our models by using a Bayesian P-value (*13*). Briefly, we computed residuals for the actual data as well as for synthetic data simulated from estimated model parameters (i.e., residuals from fitting the model to ‘‘ideal’’ data). The Bayesian P-value is the proportion of

simulations in which ideal residuals are larger than true residuals. If the model fits the data well, the Bayesian P-value is close to 0.5. Bayesian P values for our models ranged from 0.47 to 0.57 and were on average 0.51, indicating excellent model fit to the data.

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Table S1. Structure and MCMC parameter estimates for models 4-7. The MCMC P-value is twice the proportion of the posterior for which the sign was opposite to that of the mean posterior value. The MCMC P-values is not relevant for variance parameters that are constrained to be non-zero.

Model	Response	N	Distribution	Link	Effect	Mean estimate	SD of the estimate	MCMC P-value
4	Larvae count	2004	Bernoulli in ZINB	logit	Int.	-8.309	0.942	0.000
					Slope of day	-0.189	0.021	0.000
			Negative binomial in ZINB	ln	Int. no-harvest	2.081	0.251	0.000
					Int. harvest	1.006	0.244	0.000
					Slope of day no-harvest	0.001	0.001	0.380
					Slope of day harvest	0.016	0.002	0.000
					Dispersion index no-harvest	8.702	2.089	
					Dispersion index harvest	2.417	0.359	
					SD of year by pond effect (random)	0.998	0.137	
5	Standard body length	1144	Gaussian	Identity	Int. no-harvest	4.410	0.106	0.000
					Int. harvest	4.548	0.099	0.000
					Slope of age no-harvest low food	0.224	0.005	0.000
					Slope of age harvest low food	0.210	0.005	0.000
					Slope of age no-harvest medium food	0.250	0.005	0.000
					Slope of age harvest medium food	0.231	0.005	0.000
					Slope of age no-harvest high food	0.263	0.005	0.000
					Slope of age harvest high food	0.248	0.004	0.000
					Slope of age squared	-0.001	0.000	0.000
					Int. residual variance no-harvest low food	-0.021	0.157	0.854
					Int. residual variance harvest low food	-0.549	0.127	0.001
					Int. residual variance no-harvest medium food	-0.597	0.155	0.002
					Int. residual variance harvest medium food	-0.384	0.130	0.004
					Int. residual variance no-harvest high food	-0.520	0.129	0.000
					Int. residual variance harvest high food	-0.295	0.145	0.043
					Slope of age residual variance no-harvest low food	-0.005	0.003	0.079
					Slope of age residual variance harvest low food	0.011	0.002	0.000
					Slope of age residual variance no-harvest medium f	0.000	0.004	0.923
					Slope of age residual variance harvest medium food	0.010	0.002	0.000
					Slope of age residual variance no-harvest high food	0.011	0.002	0.000
					Slope of age residual variance harvest high food	-0.011	0.003	0.001
					SD of parental pair effect on int. (random)			
					SD of parental pair on slope of Age effect (random)			
6	Maturation probability	591	Bernoulli	logit	Int. no-harvest	-4.138	0.698	0.000
					Int. harvest	-4.762	0.771	0.000
					Slope of age no-harvest	-0.054	0.025	0.020
					Slope of age harvest	0.055	0.024	0.025
					Slope of length no-harvest	1.662	0.286	0.000
					Slope of length harvest	1.521	0.271	0.000
					SD of parental pair effect on int. (random)	1.470	0.356	
7	Prey count	311	Bernoulli in ZINB	logit	Int.	-1.960	0.541	0.000
					SD of individual effect (random)	0.903	0.534	
			Negative binomial in ZINB	ln	Int. no-harvest, low food	2.035	0.208	0.000
					Int. harvest, low food	1.848	0.231	0.000
					Int. no-harvest, medium food	1.928	0.245	0.000
					Int. harvest, medium food	0.986	0.286	0.001
					Int. no-harvest, high food	0.357	0.270	0.188
					Int. harvest, high food	0.672	0.309	0.025
					Dispersion index no-harvest, low food	2.388	0.722	
					Dispersion index harvest, low food	5.994	2.141	
					Dispersion index no-harvest, medium food	6.509	3.857	
					Dispersion index harvest, medium food	5.012	2.357	
					Dispersion index no-harvest, high food	2.033	0.710	
					Dispersion index harvest, high food	5.708	2.642	
					SD of individual effect (random)	0.681	0.136	