Growth and recruitment in selected lines of medaka (*Orzyias latipes*), a mesocosm experiment

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Abstract

Despite the well-known overharvested of many fish population, commercial fisheries continued to exploit populations at the same fishing rate, and has since the 1980s showed a slowly decline of 0.7 million tons fish year^{-1}. In addition, fishing practice are rarely non-random as fishing gear are usually designed to selectively remove the largest individuals that is most profitable. Due to this non-random mortality of large individuals, fisheries might induce evolutionary changes in harvested population because body size remain highly heritable. This can possibly favor genotypes with earlier maturation, smaller body size and slower growth which can ultimately lead to changes in the population dynamic of harvested populations. Harvest has shown that it can lead to changes in life-history traits of targeted species, as removal of larger individuals can lead to populations of smaller and younger individuals, reduce population abundance (density-effect) which can relax intraspecific competition and lead to faster growth and late maturation. Further, light intensity might also impact the population dynamic through climate driven changes, affecting growth and reproduction.

To analyze the effect of environmental conditions on the population dynamics from selective fishing, a large outdoor mesocosm experiment was conducted using size-selected medaka (*Orzyias latipes*), large-size harvested and small-size harvested. Further, two levels of density and light condition was implemented as environmental condition. Data was collected by visual observations of larvae, juveniles and adults to assess for the growth rate of marked adults and recruitment of larvae and juveniles. To analyze the data both generalized linear mixed models and linear models were used. According to the results, selected lines of marked adults showed no difference in growth rate, and no difference in recruitment of larvae, except at juvenile stage. Density had the strongest impact on growth rate of marked adults, showing higher growth rate at low density compared to high density. Recruitment was found highest at low density compared to high density for both larvae and juveniles. Further, light conditions showed no effect on growth rate and recruitment. These results might imply that environmental conditions did not cause great changes in growth rate and recruitment between the selected lines, but density, aside from the selected lines had great impacts on growth rate and recruitment. yet some evidence found juveniles do differ between selected lines at high density, possibly indicating that environmental conditions might cause different effects on the population dynamic from size-selective fishing.

Acknowledgments

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1 Introduction

Human impacts on the loss of biodiversity are one of the largest environmental issues faced today, which can ultimately lead to the extinction of species (Ceballos et al., 2015). Pre-human extinction rates were estimated to be 0.1 – 1 species extinction million^{-1} species year^{-1}, but current extinction rates are 100 – 1000 times higher (Chapin III et al., 2000; Ceballos et al., 2015). This current accelerated rate of biodiversity loss is mainly driven by anthropogenic perturbations such as habitat degradation, climate change, pollution and overexploitation of resources (Dirzo & Raven, 2003; Biro & Post, 2008; Ceballos et al., 2015). Resource overexploitation is widely studied, with increasing evidence that fisheries are a main concern of overexploiting resources faster than the resources can replenish itself after overexploitation (Pauly et al., 1998; Sadovy, 2001; Myers & Worm, 2003; Beamish et al., 2006). Resource overexploitation through fishery has been widely demonstrated in wild population of the sardine (*Sardinops sagax*) stocks of California in the late 1940s (Radovich, 1982), the Peruvian anchoveta (*Engraulis ringens*) in 1972 (Clark, 1976) and the Northwest Atlantic cod (*Gadus morhua*) in 1992 (Hutchings & Myers, 1994). Despite the well-known overharvested of many fish populations, commercial fisheries continued to exploit populations at the same fishing rate, and commercial fish catch from the 1980s slowly declined with 0.7 million tons year^{-1}, and the biomass of top consumers (e.g. predatory fish) has been drastically reduced by two-thirds from the second half of the 20th century (Pauly et al., 2002). Thus, the intensive fisheries management are of major interest to elucidate how harvesting impacts fish populations.

Fisheries can be direct in the way that they reduce the population abundance and biomass (Pauly et al., 2002). In addition, fishing practices are rarely non-random, because fishing gear are usually designed to selectively remove the largest individuals, that is the most profitable individuals (Law, 2000; Garcia et al., 2012; Mikko Heino et al., 2015; Breen et al., 2016; Edeline, 2016). Due to this non-random mortality of larger individuals, fisheries often induce evolutionary changes (e.g. fisheries-induced evolution) in harvested populations because body size remain highly heritable (Allendorf et al., 2008; Mikko Heino et al., 2015). Specifically, the removal of larger individuals can favor genotypes with earlier maturation, smaller body size and slower growth rate (Conover & Munch, 2002) which can ultimately alter the population dynamic of harvested population (Law, 2000; Kuparinen & Merilä, 2007;

Fenberg & Roy, 2008; Biro & Sampson, 2015). But different fishing methods also tend to catch fish with different behavioral traits, where passive fish gear (e.g. longline, traps) can catch bolder/aggressive fish, and active gear (e.g. trawls) can catch more shy fish regardless of size (Biro & Post, 2008; Mikko Heino et al., 2015). Also, anthropogenic perturbations can have severe impacts on the marine environment through exploitation of fish (M. Heino & Godø, 2002), thus it becomes crucial to understand how environmental impacts of fishing might impact the population dynamics of exploited fish population (large-sized fish *vs.* small-sized fish).

As life-history traits are key components to population dynamics (e.g. recruitment, growth, mortality), changes in life-history traits might alter the population dynamic (Jørgensen et al., 2009). Body size becomes of interest as it is an important trait that is correlated with several life histories traits, population abundance, its role in trophic interactions (Fisher et al., 2010; Schackell et al., 2010), its importance of reproductive success (Dickerson et al., 2005), and mortality as it can decreases with body size (De Roos & Persson, 2002). Harvesting has shown that it can lead to changes in life history traits of targeted species (Audzijonyte et al., 2015), as removal of larger individuals (e.g. density effect) can lead to populations of young and smaller maturing individuals who invest more of their energy into reproduction (Sharpe & Hendry, 2009; Audzijonyte et al., 2013). Also, by reducing the population abundance, the resources available can increase, thus relaxing the intraspecific competition (e.g. density-dependent effect) which can lead to faster growth rates and late maturation if maturation is size dependent (Law, 2000; Lorenzen & Enberg, 2002; Kuparinen & Merilä, 2007). Thus, decreasing the size of reproducing fish can cause a decline in the success of recruitments (e.g. larvae and juvenile), increase mortality of juveniles due to the cost of shifting more energy to reproduction, and hence, decrease the recruitment of juveniles (Longhurst, 2002; Birkeland & Dayton, 2005; Jørgensen & Fiksen, 2010). Further, light intensity (e.g. primary production) might also impact the population dynamic, through climate-driven changes, affecting growth and reproduction (Rjinsdorp et al., 2009). Competition for resources can be the ultimate factor for density-dependent growth or survival (Post & Johnston, 1999). This is common in size-structured populations as size among individuals can influence the outcome of competition among individuals (Tonn et al., 1994). Exploitative competition can result in reduced growth rate when food resources are limiting, while the reverse is interference competition where larger body size is advantageous (Post & Johnston, 1999). If food

resources are limited, cannibalism might arise as the ultimate interference competition, but the intensity of cannibalism depends on the relative size of individuals (Baras & Jobling, 2002). thus, assessing the potential effects of environmental conditions in the context of selective fisheries, are of interest to further understand what the consequences might be of changes in the population dynamics.

The objective of this study was to investigate how environmental impacts of fishing could affect the population dynamics of two size-selected lines representing the effect of selective fishing on body size. We used experimental medaka originated from a size-dependent bidirectional selection experiment to create two size-selected (large-size harvested and small-size harvested) lines. The species model Medaka, is a small freshwater fish (adult size: 15~35 mm) captured in Toyohashi, Japan (Kinoshita et al., 2009). Further, two density treatments (high and low density) representing the fisheries effect and two light treatments (high and low primary production) representing the climate driven changes in primary production was crossed with the size-selected lines. This created six replicates to assess the impacts of fisheries and environmental changes on population dynamics (e.g. recruitment, growth, mortality). From this I aim to answer the following question:

- Will there be a difference in growth rate and recruitment between the two size-selected lines?

- Will differences in density have divergent effects on growth rate and recruitment for the two size-selected lines?

- Will differences in light intensity have divergent effects on growth rate and recruitment for the two-size selected lines?

2 Material and Methods

2.1 Study species

Medaka individuals used in this study derived from 100 breeders initially captured in 2011 in wild populations located in Kiyoshu (Toyohashi, Japan). These initial breeders and their progeny were transferred to France and stocked in large outdoor mesocosms at the Center of Experimental and Predictive Ecology (CEREEP Ecotron Ile-de-France, http://www.foljuif.ens.fr/). The medaka is an ideal model organism for experiments due to its short life-cycle (2-3 months), large thermal tolerance (4 - 40^{o}C), and easy breeding in both laboratory tanks and outdoor ponds (Kinoshita et al., 2009). In April 2013, around 100 individuals were randomly selected and transferred into 3L-tanks (10 - 12 fish per tank) at the aquarium facility (temperature: 26^{o}C, photoperiod: 14/10h) to control for both environmental conditions and parental effects. Fish were fed *ad libitum* with a mixed diet of dried and living (*Artemia salina and/or Turbatrix aceti*) food. These laboratory conditions provided optimal growth and maturations conditions to medaka (Kinoshita et al., 2009). Importantly, individuals from the same family (i.e., originated from the same breeders) were raised together.

2.2 Bi-directional selection – producing two size-selected lines

A bi-directional selection on standard body length (sbl) of mature individuals was applied here to produce two lines: a small-size harvested line (SH), and a large-size harvested line (LH) (Renneville, 2016). The large-size harvested line (LH) mimics the harvesting from fisheries, as fisheries are usually selective towards harvesting larger individuals due to, e.g., their higher economical value (Mikko Heino et al., 2015). Thus, the small-size harvested line (SH) represents a reversed form of fishing (removal of smaller individuals). Individuals were exposed to size selective harvest through several generations (from F1 to F11), where the small-size harvested line (SH) contained only large individuals that were allowed to reproduce, while the large-size harvested line (LH) contained individuals of smaller size allowed to reproduce (see details (Renneville, 2016). Specifically, at 60 day-post-hatch (dph), fish were measured under a binocular for standard body length (sbl ± 1 mm) and a family-level selection was applied based on the average sibling sbl (Renneville, 2016). For each line, 10 families were selected: families with the highest sbl for small-size harvested line (SH) and families with lowest sbl for large-size harvested line (LH). Then, at 75 dph, fish from the previously selected families were measured and sexed (Fig. 2.2). For each family, 2 or 3

individuals of each sex were selected as subsequent breeders: largest individuals for the small-size harvested (SH) and smallest individuals for the large-size harvested (LH) (Fig. 2.1). Siblings from a breeding pair were raised in the same tank at constant density (14 - 17 individuals per 3L-tank). Fish were hand-fed *ad libitum* with a mixed diet of dry food (GM300 and GM150; Retch, Germany) and living *Artemia salina*. The use of identical rearing conditions (temperature: 26°C, photoperiod: 14/10h) ensured that observed differences between the two lines were genetic rather than environmental (Conover and Munch 2002).

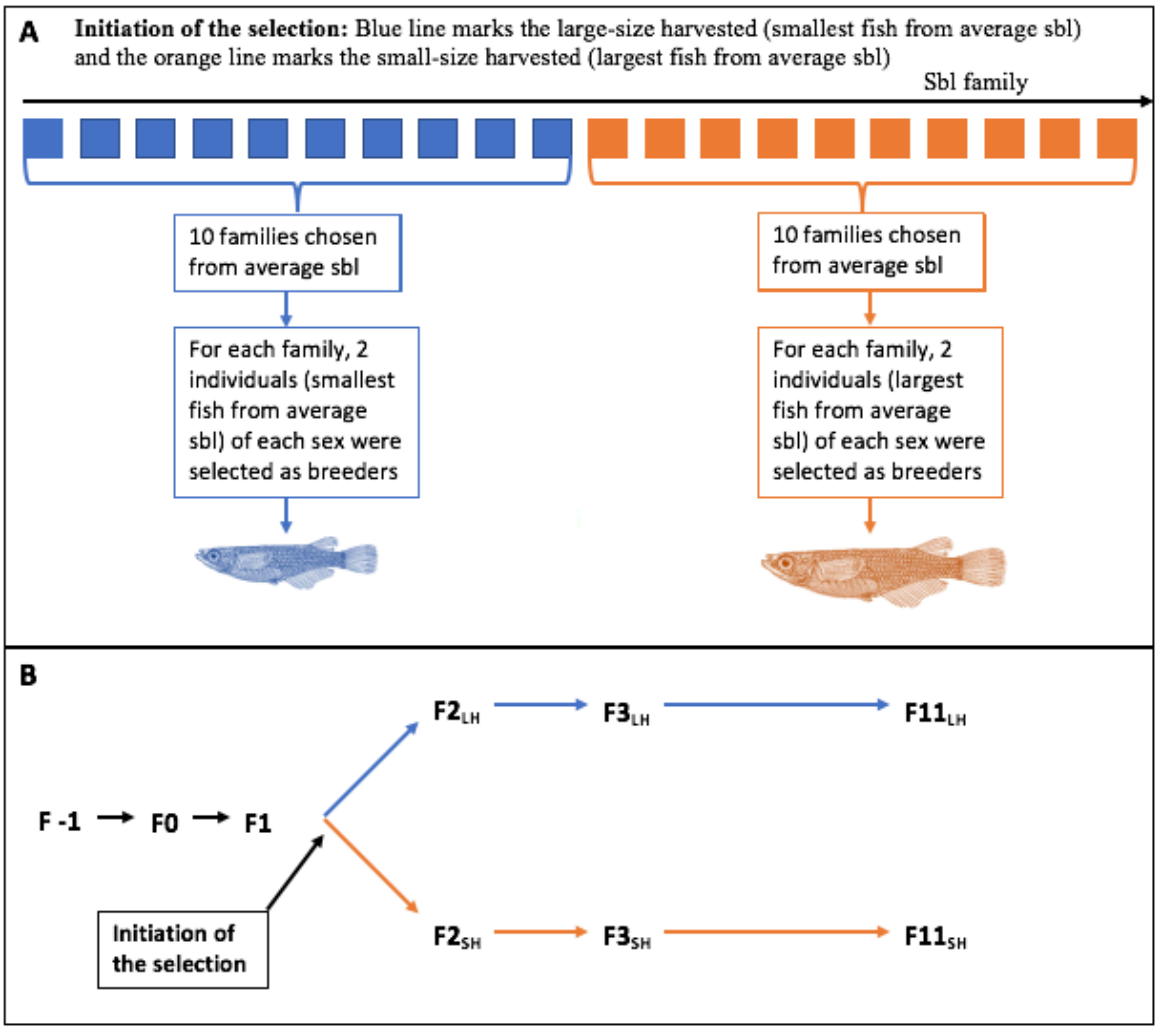

Figure 2.1: Bi-directional selection on standard body length (sbl) of mature individuals applied to produce two lines: small-size harvested (SH) and large-size harvested (LH). Schematic representation of (A) the selection for small-size harvested (SH) and large-size harvested (LH), and (B) the initiation of the selection. Adapted from Renneville 2016. Picture of the medaka fish (*Oryzias latipes*) adapted from (Iwamatsu, 2004).

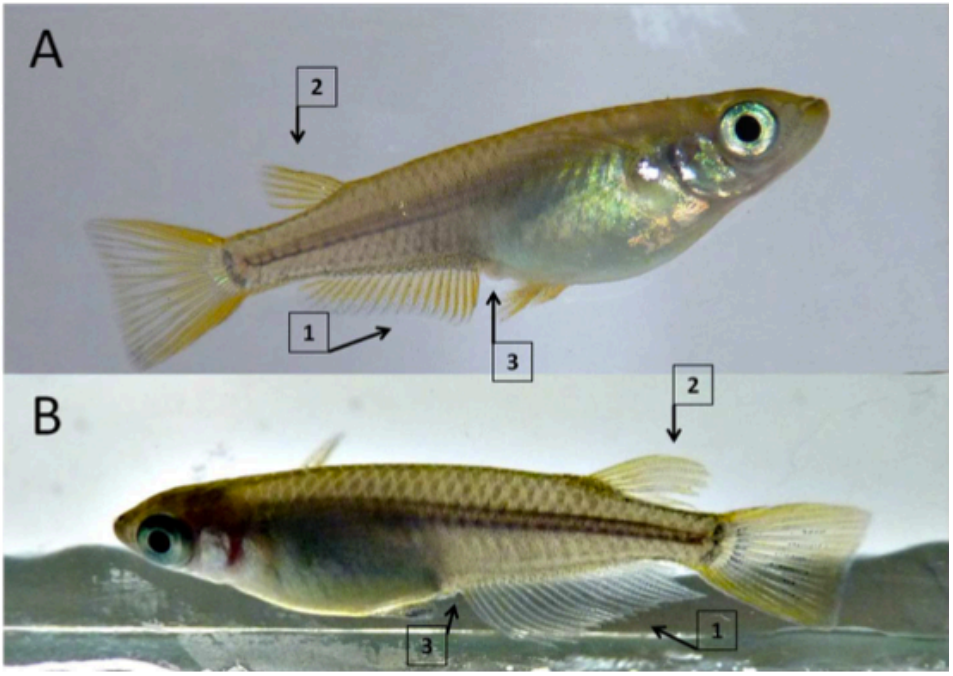

Figure 2.2: Picture of a female (A) and a male (B) medaka fish. The anal fin (1), the dorsal fin (2), and the shape of the urogenital papilla (3) are external sexual characteristics that differentiate them. Adapted from Renneville 2016.

2.3 Experimental fish populations

On the 27th of June 2017, fish from F11 were anesthetized with MS-222 (tricaine methane sulfonate), weighted ($W_i \pm 0.1$g), measured for standard length ($sdl_i \pm 1$ mm) and sexed. In each harvested line, fish from 16 – 21 mm sdl were selected to minimize differences in standard length (sdl) between lines (mean SH = 19.4 mm ± 1.4 SD; mean LH sdl = 18.9 ± 1.3 SD). Males and females were then used to create artificial populations using combinations of different families to minimize inbreeding (mean kinship coefficient = 0.17 ± 0.1 SE and 0.23 ± 0.1 SE in SH and LH populations, respectively). Within each population, fish were individually marked above the lateral line using visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, WA, USA) to render each fish individually identifiable (Fig. 2.3). After being marked, fish were placed in well-oxygenated water and released into new laboratory tanks (i.e., one for each experimental population) after their full recovery. Markings of the fish were checked before being released into the outdoor mesocosms.

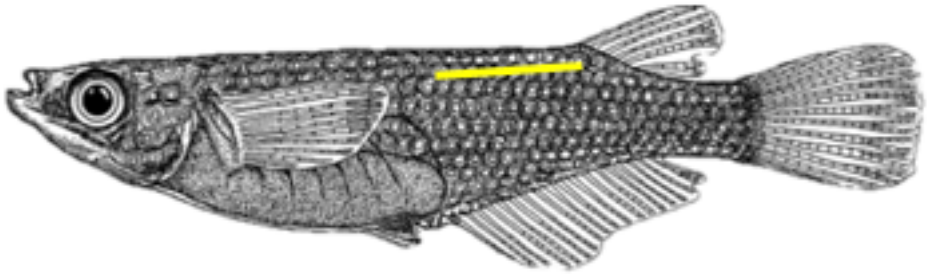

Figure 2.3: Illustration of marking using visible implant elastomer (VIE). Figure adapted from (Iwamatsu, 2004).

2.4 Experimental design

A 3-month experiment was conducted at the CEREEP using 48 outdoor mesocosms circular cattle tanks (500 L, 0.79 m deep, 1.04 m diameter) arranged in 5 blocks (Fig 2.4A). The experimental design was composed of eight treatments using a full factorial design where selected lines (SH and LH), light intensity (high light - HL and low light - LL) and the density of fish (high density - Hd and low density - Ld) were crossed, and each treatment replicated six times. Light intensity was manipulated using nets with different mesh size that allowed the passage of 70% (low light) and 92% (high light) ambient light. High- and low-density treatments consisted of 12 and 3 fish, respectively, with a constant sex ratio (8F:4M and 2F:1M, respectively). We kept a constant sex ratio for high- and low-density as differences in sex ratio could have different ecological effects (Fryxell et al., 2015).

In early April 2017, each mesocosm was filled with a mix of dechlorinated tap water (100 L) and filtered oligotrophic water (300 L; filtered to remove zooplankton and debris) from a local storage pond. Zooplankton was collected from local ponds using nets (mesh size: 50µm), separated from debris by a small sucking tube before being homogenized and a mixture of 2 L was added in each mesocosm. Each mesocosm was also supplied with 2 L of sediment mixture (including live invertebrate larvae), collected from local outdoor mesocosms. Finally, each mesocosm was covered with a net (*see details above*) and given 3 months to mature before medaka were introduced. In early July 2017 two floating shelters made of wool (length: 31 cm) and two floating plastic thread (width: 31 cm, length: 20 cm) were added in each mesocosm to provide spawning substrate and protection for larvae, respectively (Fig 2.4B). Importantly, in mid-June 2017, mesocosms were enriched with a

liquid mixture of potassium phosphate (KH_2PO_4) and sodium nitrate ($NaNO_3$) (concentration: 1L osmosis water with 9.717 g KH_2PO_4 and 2 × 126.463 g $NaNO_3$) (Leflaive et al., 2008).

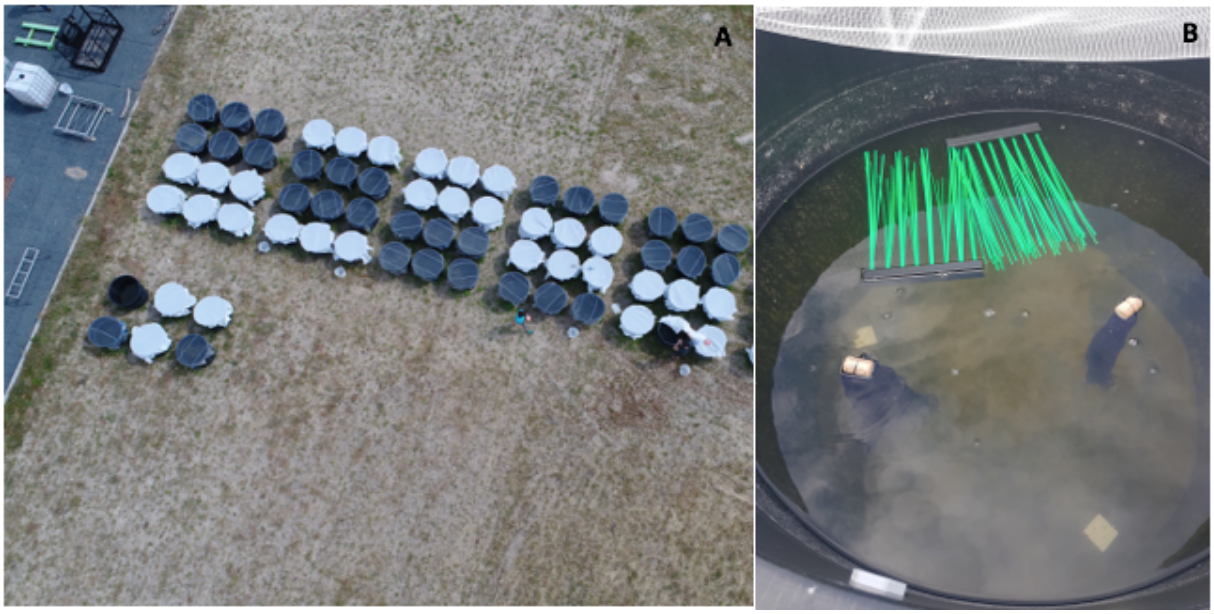

Figure 2.4: (A) Aerial picture of the mesocosms arranged in 5 blocks; (B) Representation of mesocosms content, where floating wool shelters and floating plastic threads were added to provide spawning substrate and protection for larvae, respectively.

2.5 Measurements during the experiment

For each mesocosm, the number of fish was quantified from count data based on visual observations. During each count event (visual observations), fish from each size category (i.e., larvae, juvenile and adult) were counted, and this approach was used to reduce stress due to handling (B. A. Barton & Iwama, 1991). Specifically, every two weeks, one counting event was conducted over two days (from mid-July to mid-September; Table 2.2) and replicated three times per day during morning (around 9:00 pm), noon (around 12:00 pm am) and mid-afternoon (16:00 am). The time spent on each mesocosm was reduced to 3 min to standardize the sampling effort. Two different size ranges (Fig. 2.5) were used in assessing the different stages of young medaka fish as adults were easily distinguished from larvae and juvenile. Further, adult counts were excluded from further analysis as very few new adults were observed during the experiment.

At the end of the experiment on the 25th of September, each mesocosm was drained and fish were collected using a hand net and measured for final sdl (sdl_f ± 1mm) and weight (W_f ± 0.1

g). For each recaptured marked fish (Fig. 2.3), the specific growth rate of length (mm % month^{-1}) (Jobling, 1983) was calculated as follows:

$$SGR = \frac{\ln(sdl_f) - \ln(sdl_i)}{t} \times 100$$

The specific growth rate was calculated to obtain the growth in length for the marked recaptured fish during the experiment (t = 3 months). The size-harvested lines had minimal size difference in length at start (see *experimental fish population*), thus the use of length to assess growth during the experiment for the different treatments (Line, Density, Light) might be a good approach. All recaptured fish were euthanized with an overdose of MS-222 and measured (± 1 mm; ± 0.1 g).

For each mesocosm, temperature (^{o}C) and chlorophyll-*a* concentration (µg/L^{-1}) were obtained using a portative probe (Yellow Spring Instrument; Yellow Spring, OH, USA; multiparameter sonde). With the use of the portative probe, one measurements were conducted at mid-depth for each mesocosm. This approach was conducted every two weeks (Table 2.2).

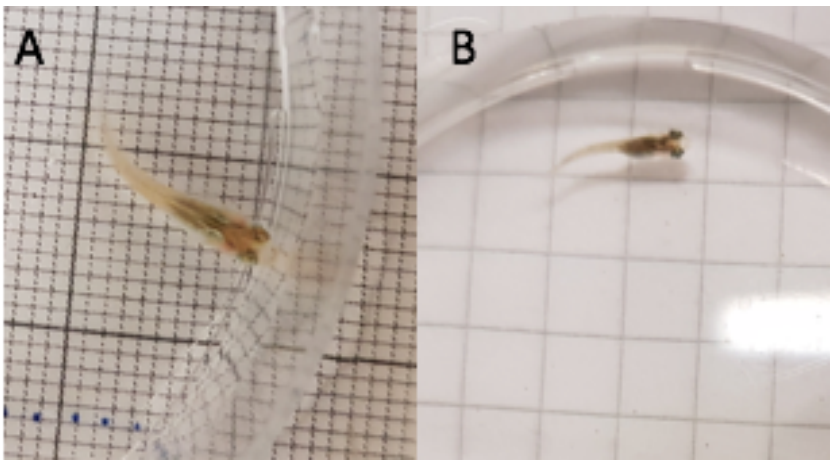

Fig. 2.5: Pictures of larvae and juvenile medaka**.** (A): 28-35 dph juvenile (11 - 14 mm); (B): 13-18 dph larvae (7 – 9 mm).

Table 2.2: Timeline of measurements and visual observation (counting of individual fish in the mesocosms) conducted during the experiment; X – not conducted

Date	Fish	Temperature	Chlorophyll-a
19.06.17	X	Measured	Measured
05.07.17	Released to their respective mesocosms	X	X
10.07.17	X	Measured	Measured
13.07.17	Test of protocol for visual observation (counting)	X	X
18-19.07.17	Counted	X	X
24.07.17	X	Measured	Measured
01-02.08.17	Counted	X	X
08.08.17	X	Measured	Measured
16-17.08.17	Counted	X	X
21.08.17	X	Measured	Measured
29-30.08.17	Counted	X	X
04.09.17	X	Measured	Measured
12-13.09.17	Counted	X	X
18.09.17	X	Measured	Measured
20-21.09.17	Draining of mesocosms and recapture of all individuals	X	X
24-25.09.17	All fish measured and weighted (± 0.1 g) to nearest mm (±1 mm) before MS-222 overdose	X	X

2.6 Analysis

All the figures and statistical analyses were performed in Rstudio version 1.1.423. (Rstudio Team, 2016). Similarly, all linear models (LMs) were checked for normality and homoscedasticity using diagnostic plot to visualize the model fit.

2.6.1 Environmental conditions

I tested for variation in temperature (^{o}C) and chlorophyll-*a* concentration (µg L^{-1}) using linear models, with blocks (for temperature) and treatments (for chlorophyll-*a* concentration) as explanatory variables. Blocks as an explanatory variable was used as mesocosms was arranged in blocks (A, B, C, D, F) across a field (Fig. 2.4A). Treatments as an explanatory variable was used as the treatments (Line, Density and Light) could influence the chlorophyll-*a* concentration. Further, date (sampling events) was added as an explanatory

variable to assess temporal trends. Date (sampling event) was also used for chlorophyll-*a* concentration to assess if changes in chlorophyll-*a* concentration for the treatments varied over time. The full models used for Temperature (^{o}C) and chlorophyll-a concentration:

$$\text{Temperature} \sim \text{Blocks} \times \text{Sampling event}$$

$$\text{Chlorophyll} \sim \text{Treatment} \times \text{Sampling event}$$

2.6.2 Specific growth rate of length (SGR, % month^{-1})

I tested for variation in growth of the marked adults fish using general linear models. The different treatments (Line, Density and Light) were included as main effects, together with two two-way interactions of particular interest (Line × Density + Line × Light). These interactions were of interest as I wanted to assess if the growth difference in size-harvested (small-size harvested – SH; large-size harvested - LH) lines interacted with the main effects of density (high and low density) and light (high and low light attenuation). A backward selection procedure (Crawley, 2007) was conducted, starting with the full model with interactions, and further removing interaction terms subsequently from the model if the interactions were non-significant. The full model used for specific growth rate in length (SGR, % month^{-1}):

$$\text{SGR} \sim \text{Line} \times \text{Density} + \text{Line} \times \text{Light}$$

2.6.3 Effect of treatments at sampling events and presence of larvae and juvenile

Variation in the number of larvae and juveniles was checked against each sampling event to test which treatment was significant at that particular time event. From this I used the highest number of larvae and juveniles from each mesocosm to represent the highest possible abundance of larvae and juveniles. Further, the probability of presence (presence/absence) of larvae and juveniles was tested using the converted counts as binary data (presence (1) / absence (0)), to test for the probability of presence for the whole experiment.

Recruitment was measured as the presence of larvae and juvenile individuals. To test for the effect of treatments (Line, Density and Light) on the presence of larvae and juveniles I used a generalized linear mixed effects model (GLMM) using the function glmer () with binomial

distribution and logit-link in the R-package lme4(version 1.1-19) (Bates et al., 2015). Tank ID was used as a random effect to account for pseudo-replication. A general linear model was also used to test if changes in the number of larvae and juveniles observed differed significantly between treatments (Line, Density and Light) at each sampling event during the experiment. Likewise, for the specific growth rate in length (SGR, % $month^{-1}$) two two-way interactions of particular interest were included in the full models for the presences of larvae and juvenile (GLMM) and counted larvae and juvenile (glm), as I wanted to assess if size-harvested line interaction with density and light had any impact on the probability of finding larvae and juvenile. Also here a backward selection procedure (Crawley, 2007) was used to find the final model.

Normality and homoscedasticity were checked for larvae and juvenile (only for presence model GLMM, count model followed same checks as e.g., temperature) using the package (dHARMa; version 0.2.0) (Hartig, 2018) that supports diagnostic checks for models of GLMM. The dHARMa package was chosen as it runs a simulation-based approach that makes interpretable residuals for fitted GLMM, assessing the residuals to the fitted model (Hartig, 2018). R-squared for GLMM were obtained using the r.squaredGLMM from the package MuMIn (K. Barton, 2018). Specifically, the marginal (Rm^2; proportion of the variance explained by fixed effects) and the conditional (Rc^2; proportion of the variance explained by both fixed and random effects) were calculated (Nakagawa & Schielzeth, 2012). Further, if interactional terms were significant, a post-hoc test was performed using the package (emmeans; version 1.3.0) with the function pairs() (Russell, 2018) to investigate which interactional term was significant.

The full models for larvae and juvenile (presence model; GLMM):

$$\text{Larvae} \sim \text{Line} \times \text{Density} + \text{Line} \times \text{Light} + (1|\text{TankID})$$

$$\text{Juvenile} \sim \text{Line} \times \text{Density} + \text{Line} \times \text{Light} + (1|\text{TankID})$$

The full models for larvae and juvenile at each sampling event (count model; glm):

$$\text{(Larvae) T0 - T6} \sim \text{Line} \times \text{Density} + \text{Line} \times \text{Light}$$

$$\text{(Juvenile) T0 – T6} \sim \text{Line} \times \text{Density} + \text{Line} \times \text{Light}$$

3 Results

3.1 Environmental conditions

The mean temperature (°C) in the mesocosms was very high (~28 °C ± 0.1 SE) during the start of the experiment, but decreased rapidly reaching low temperature (~15 °C ± 0.07 SE) at the end of the experiment period (Fig. 3.1; Appendix A, Table 2.A). Temperatures were very similar among the five blocks. Temperature did differ significant between blocks (Table 3.1). Further analysis showed that block F tended to be slightly warmer (P-value = 0.013) than block A (intercept), while the other blocks (B, C, D) did not differ from A (Appendix A, Table 1.A).

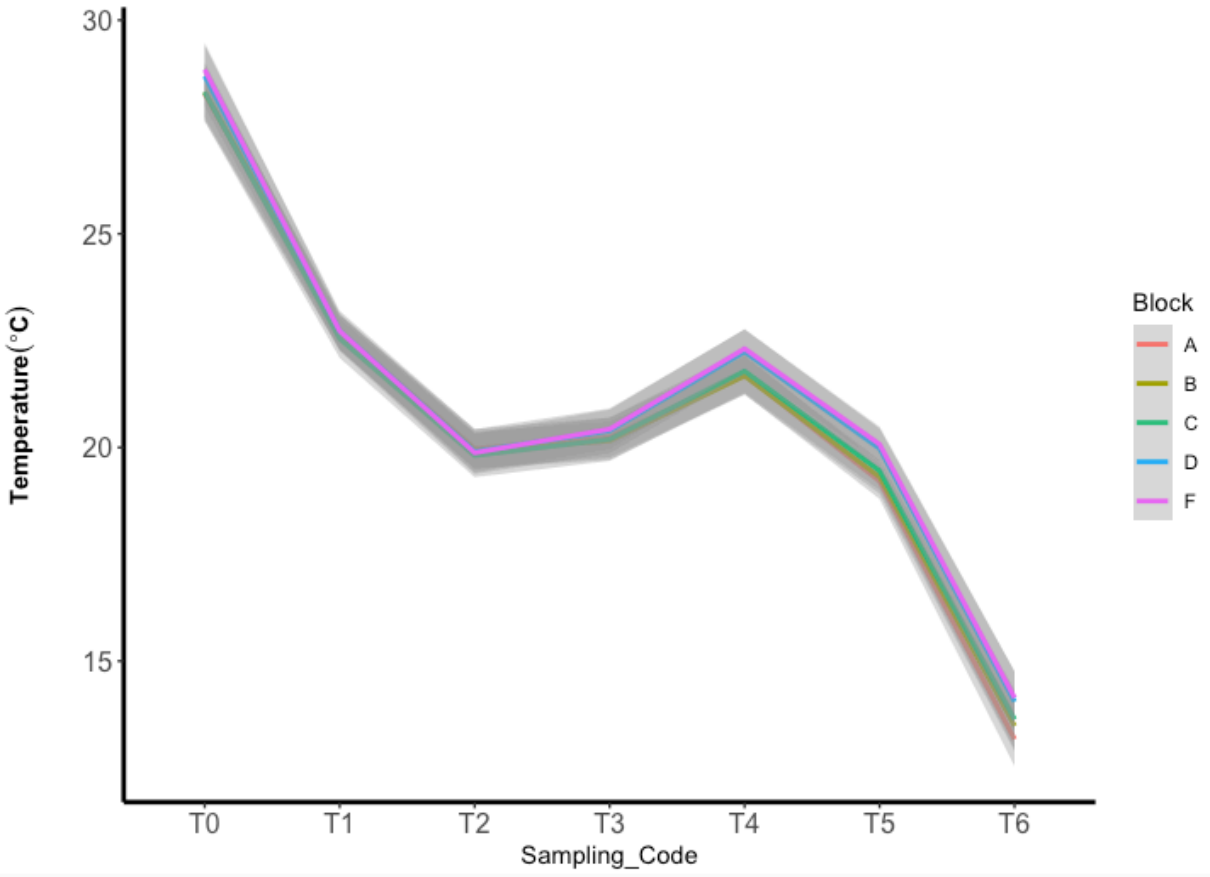

Figure 3.1: Temperature (°C) measured for all the 5 blocks (A, B, C, D, F) during the experiment at each sampling event (T0-T6). Blocks are represented by colored lines and grey shading indicates confidence interval. (**T0** – 19.06.17; **T1** – 10.07.17; **T2** – 24.07.17; **T3** – 08.08.17; **T4** – 21.08.17; **T5** – 04.09.17; **T6** – 18.09.17)

Table 3.1: Results of the linear model used to test for temperature (^{o}C) variance against the explanatory variables blocks (A, B, C, D, F) and sampling event (T0 - T6). Significant P-values are represented in bold.

Temperature(^{o}C)		Df	Sum Sq	Mean Sq	F-value	P-value
	Block	4	12.3	3.08	10.782	**<0.001**
	Sampling event	6	6019.8	1003.31	3511.12	**<0.001**
	Block:Sampling event	24	8.6	0.36	1.25	0.193
Chlorophyll-*a* concentration (µg/L^{-1})						
	Treatment	7	494.7	70.67	4.82	**<.0.001**
	Sampling event	6	938.0	156.33	10.66	**<0.001**
	Treatment:Sampling event	42	698.6	16.63	1.13	0.272

Chlorophyll-*a* concentration (µg/L^{-1}) in the different treatments was around 2~4 µg/L^{-1} at the start of the experiment, tended to increase at later sampling events (from T1 – T4) before decreasing at the end of the experiment (Fig. 3.2; appendix A, Table 3.A). Several of the treatments showed similar trends of increasing chlorophyll-*a* concentration at start, and decreasing towards the end of the experiment, but some treatments showed larger fluctuation of chlorophyll-*a* concentration (µg/L^{-1}) (Fig. 3.2).

The model (Table 3.1) shows that chlorophyll-*a* concentration significantly varied between treatments and each sampling events. Treatments with high light (HL) attenuation and low light (LL) attenuation varied in chlorophyll-*a* concentration at different sampling events, but high light attenuation showed higher variations at different sampling events than low light attenuation (Fig 3.2). Variation of chlorophyll-*a* concentration between treatments throughout the experiment (T0 – T6) was found to be non-significant (Table 3.1).

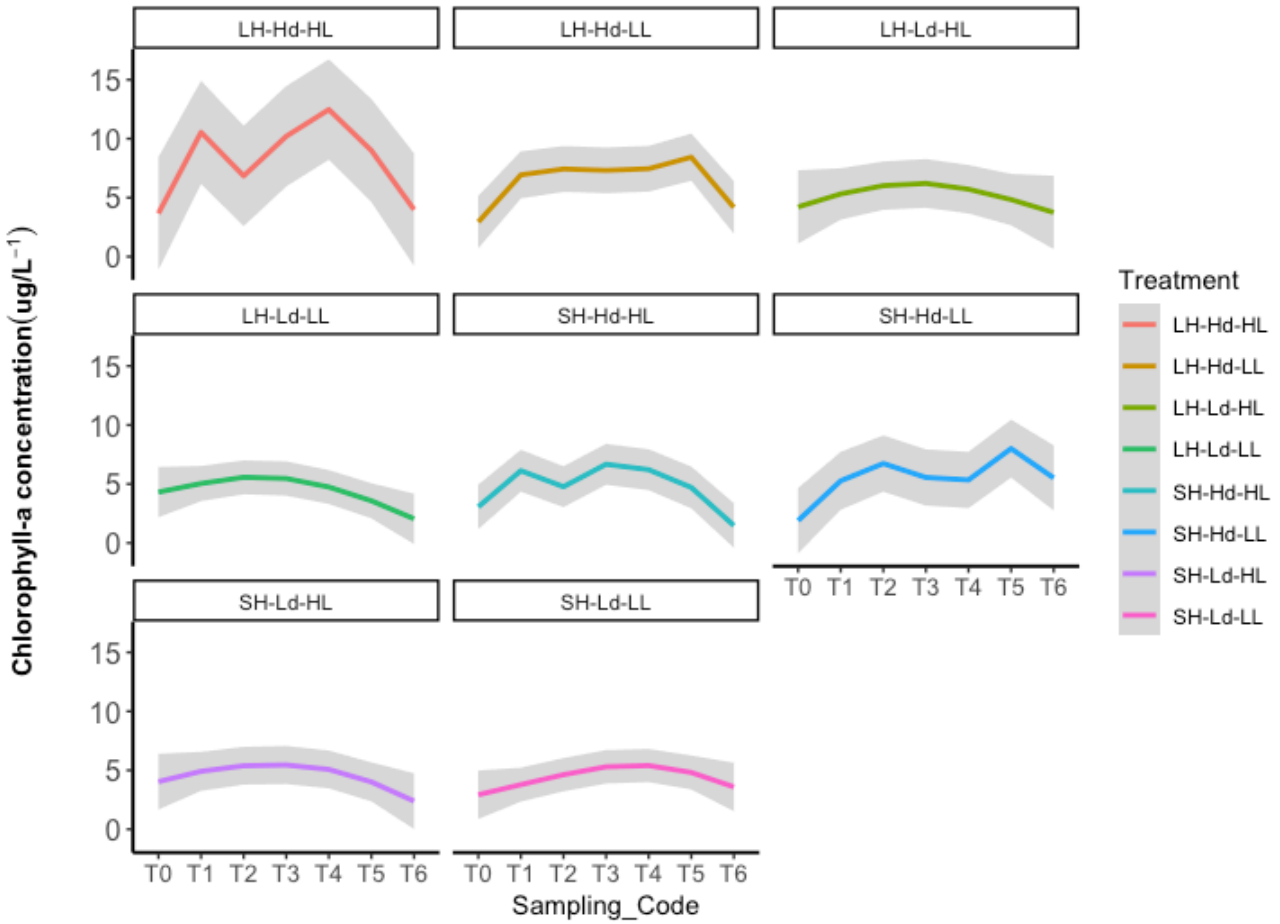

Figure 3.2: Chlorophyll-*a* concentration ($\mu g/L^{-1}$) for every treatments during the experiment at each sampling sampling event (T0 – T6). Treatments are represented by colored lines and grey shading indicates confidence interval. (**T0 –** 19.06.17; **T1 –** 10.07.17; **T2 –** 24.07.17; **T3 –** 08.08.17; **T4 –** 21.08.17; **T5 –** 04.09.17; **T6 –** 18.09.17). Treatments represents the possible combination of Line (LH and SH), Density (Hd and Ld) and Light (HL and LL), giving eight different treatments.

3.2 Specific growth rate for length (SGR, % month^{-1})

Measured marked individuals at the start of the experiment was recaptured at the end of the experiment, were a large number of marked individuals was recaptured (Appendix B, Table 2.B).The mean standard body length (sdl) shown from the recaptured individuals at the end of the experiment shows an increase in body length during the experiment, with low variation between lines (LH and SH) and light (HL and LL), but a high variation between density (Hd and Ld) (Appendix B, Table 2.B).

The model (Table 3.3; parameter estimates in Appendix B, Table 1.B) showed no significant effect of line (small-size harvested - SH and large-size harvested - LH) and light (high light - HL and low light - LL) on the specific growth rate for length (SGR, % month^{-1}; fig 3.3), but there was a highly significant effect of density. The marked fish grew faster at low density (Ld) than at high density (Hd) (Fig. 3.3; Appendix B, Table 2.A for the estimates).

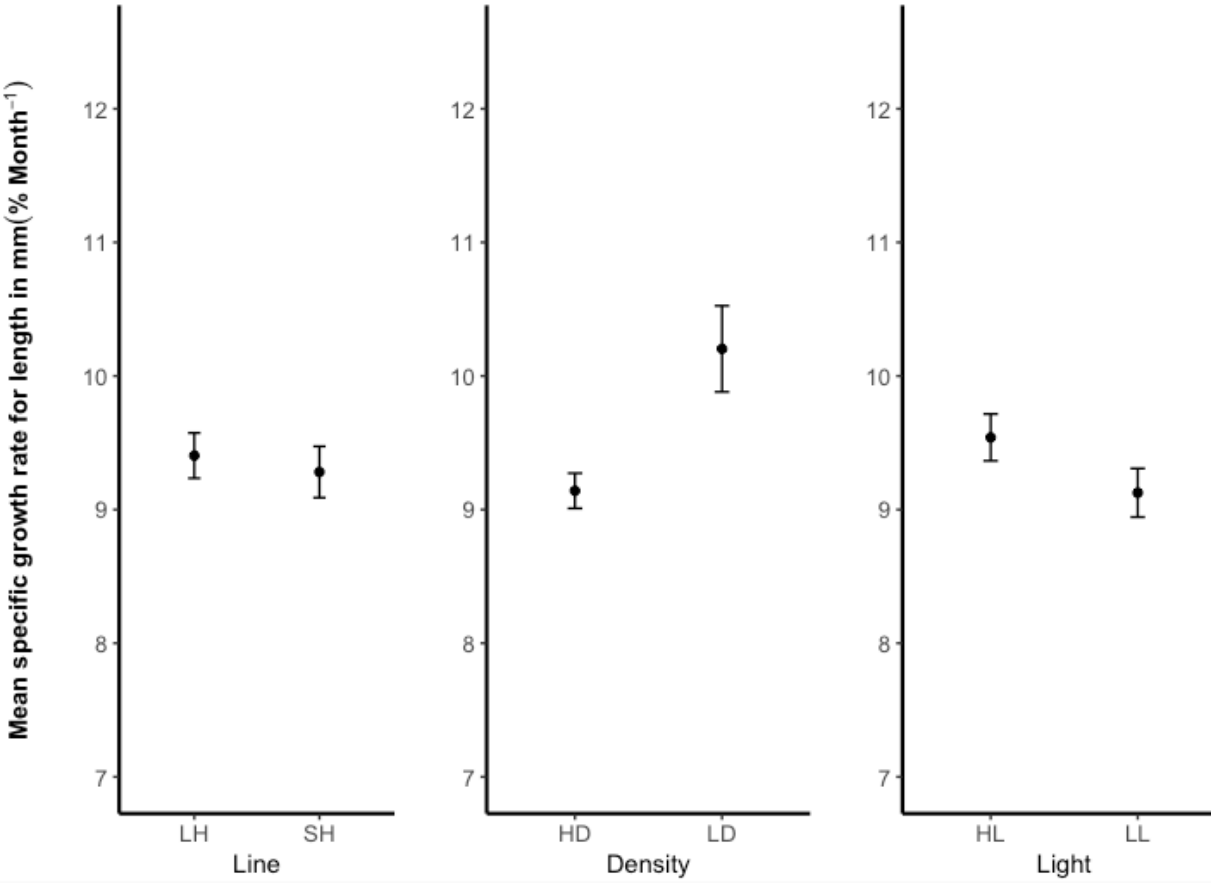

Figure 3.3: The mean ± se specific growth rate for length in mm (SGR, % month^{-1}) shown as mean ± SE for the lines (LH – Large-size harvested; SH – Small-size harvested), density (HD – High Density; LD – Low Density) and light (HL – High Light; LL – Low Light).

Table 3.3: Results of the linear model used to test for the specific growth rate for length in mm (SGR, % month^{-1}) against the different treatments (Line, Density and Light). Significant P-values are presented in bold.

SGR% month^{-1}		**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**P-value**
	Line	1	15.47	15.47	1.93	0.162
	Density	1	1252.20	1252.20	156.62	**<0.001**
	Light	1	0.01	0.01	0.00	0.978

3.3 Presences of larvae and juvenile

At the first count at sampling event (T0), two weeks after the start of the experiment, high number of larvae were observed in the mesocosms. Sampling event T0 – T4 represents the start and end of the observations of larvae and juvenile, and are not to be confused with T0 – T6 from measurements of temperature and chlorophyll-a which started earlier. From T1 onwards the numbers decreased and were low at the end of the experiment (Fig. 3.4). No juveniles were observed at the two first sampling events (T0 – T1), before being observed at sampling event T2 - T4 (Fig. 3.5).

From the estimate table (Appendix C, Table 1.C), Density was found to have a significant effect on the number of larvae observed at every sampling event (T0 – T4) during the experiment (Appendix C, Table 1.C). From this, the highest abundance observed of larvae was at low density compared to the abundance of larvae observed at high density (Fig 3.4) Line had a significant effect on the observations of larvae at the start of the experiment, but showed no significant effect on the observations of larvae near the end of the experiment (Appendix C, Table 1.C). For juveniles, both line and density had a significant effect on the number of juveniles observed at each sampling event (T2 – T4) during the experiment. This shows that the observations of juveniles were higher at small-size harvested line compared to the observations of juveniles from large-size harvested line (Fig 3.5). Further, this also shows juveniles were observed more frequently at low density compared to high density (Fig 3.4). The interaction between Line and Density also had a significant effect on the observation of juvenile during the experiment (T2 – T4) (Appendix C, Table 2.C), were observations of large-size harvested line was lower at high density compared to small-size harvested line.

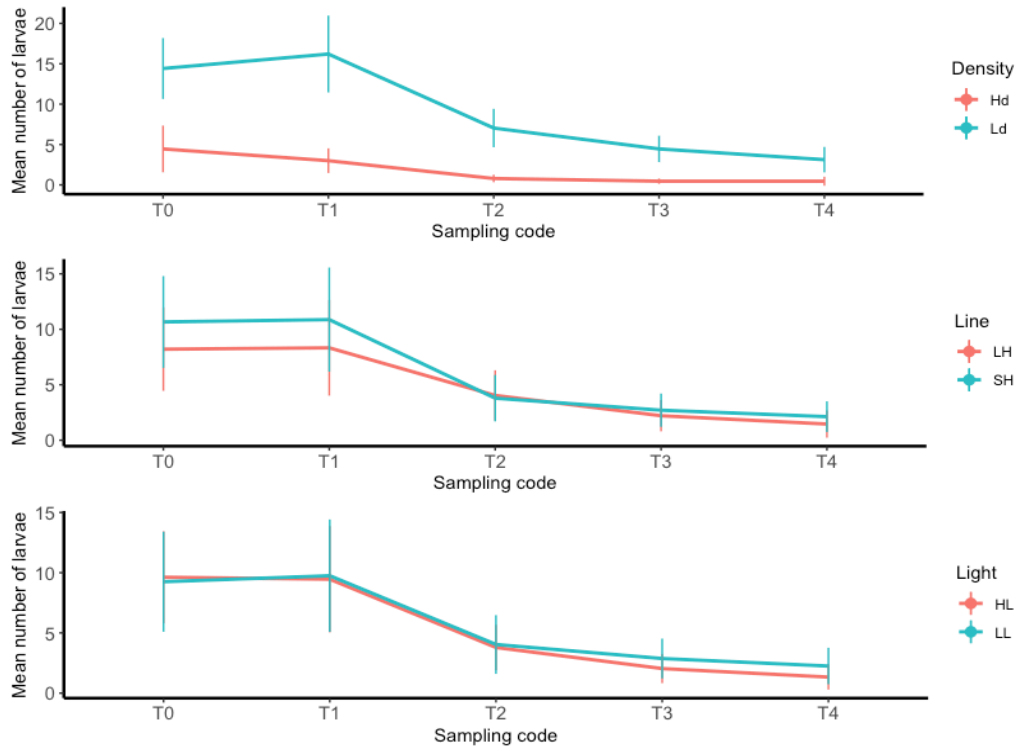

Figure 3.4: The mean observed larvae for each treatment (Line, Density and Light) at each sampling event throughout the experiment. Upper and lower lines at each sampling event (T0 – T4) represent the standard deviation.

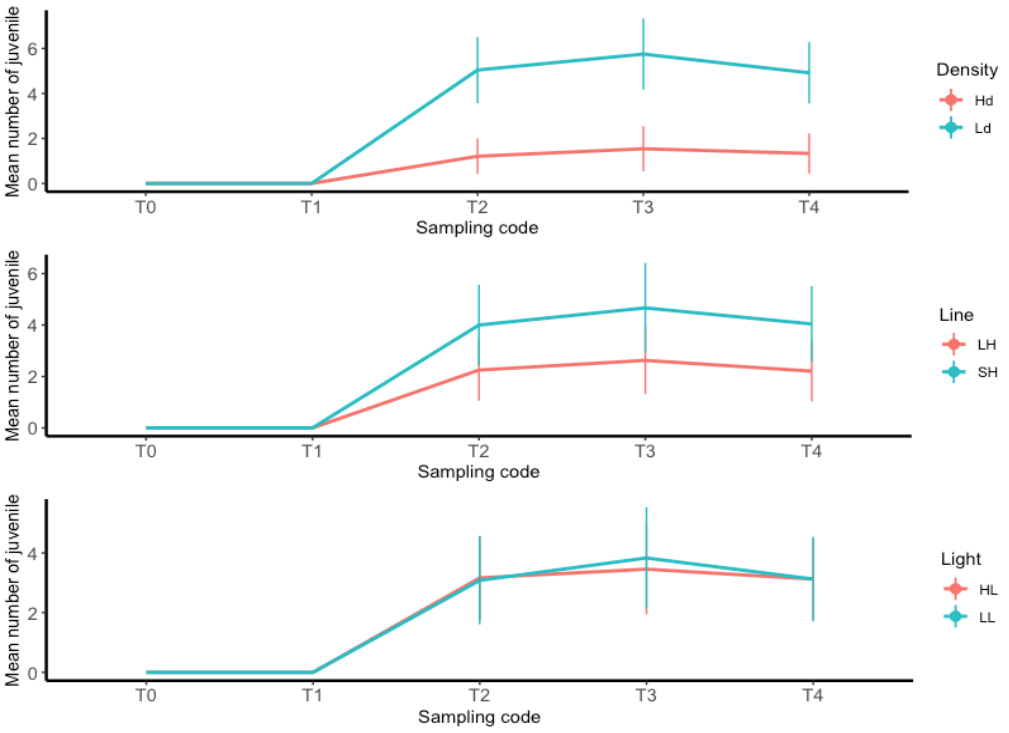

Figure 3.5: The mean observed juvenile for each treatment (Line, Density and Light) at each sampling event throughout the experiment. Upper and lower lines at each sampling event (T0 – T4) represent the standard deviation.

The probability of larvae presence conducted for the whole experiment found from the model (Table 3.4) that, neither line, nor light (Table 3.4) had a significant effect on the predicted probability of observing larvae during the experiment. Density showed a significant effect (Table 3.4) on the predicted probability of observing larvae during the experiment, where the probability of observing larvae was almost 3 times higher at low density (Ld) than at high density(Hd).

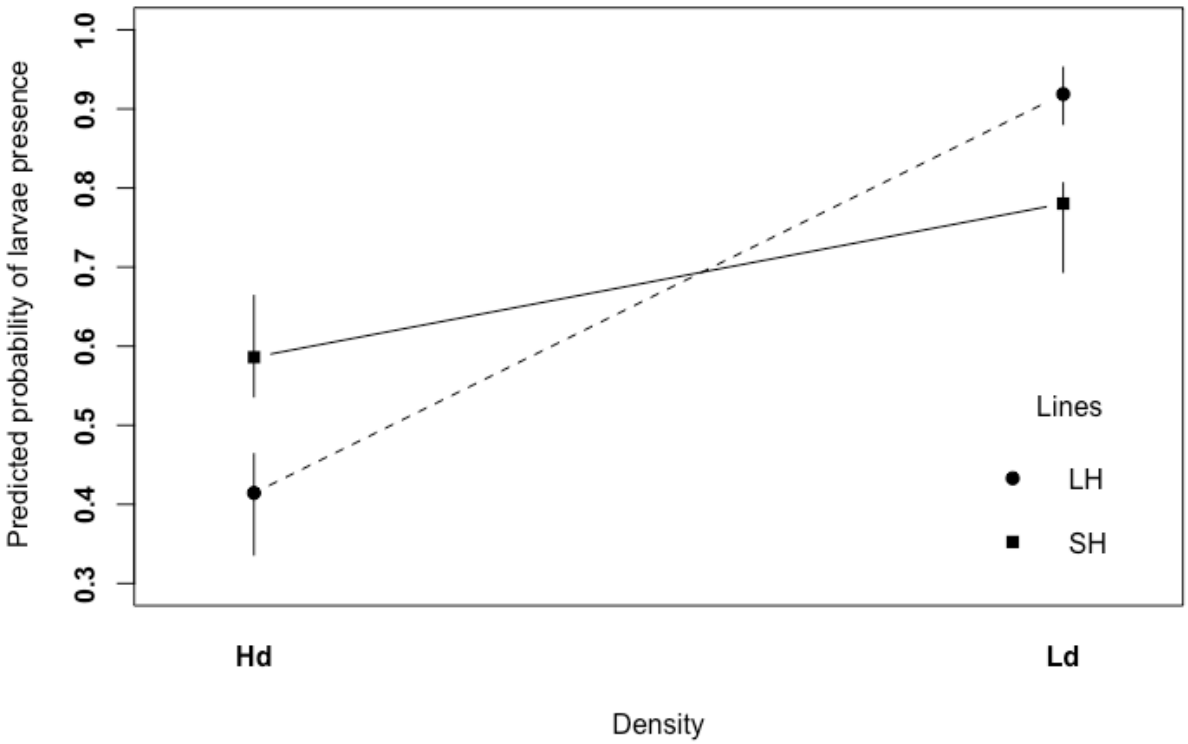

Figure 3.6: The explanatory variables (Line, Density and Shadow) tested against the probability of larvae presence. Lines crossing the points of SH and LH represents standard error lines. Hd – high density; Ld – Low density; LH – large-size harvested; SH – small-size harvested.

Table 3.4: Summary for the generalized linear mixed model used to test the effects of explanatory variables (Density, Light and Line) on the presence of larvae. SH – Small-size harvested; LH – large-size harvested; Hd- High density; Ld – low density; HL – high light; LL – low light. Significant P-values are represented in bold.

Larvae		Chisq	Df	P-value
	Line	0.01	1	0.890
	Density	11.92	1	**<. 0.001**
	Light	0.02	1	0.867
	Line:Density	2.72	1	0.098

For analyzing the predicted probability of observing juveniles for the different treatments (Line, Density and Light) during the experiment, same procedures were conducted here as for the probability of observing larvae. The full model with the interactions of interest was reduced to a model containing only one significant interaction (Line*Density), this model was further used in the analyzes. Light had no significant effect on the predicted probability of observing juveniles during the experiment (Table 3.5). Both line and density showed significant effect on the predicted probability of observing juveniles, where the probability of observing juveniles for small-size harvested (SH) line was two times higher compared to large-size harvested (LH), and three times higher at low density (Ld) compared to high density (Hd) (Table 3.5; Fig. 3.7). Further, an interaction effect between line and density was found to be significant (Table 3.5), further post-hoc analysis found significant difference in juvenile presence between the lines at high density (P-value 0.005), but no significant differences at low density (P-value 0.802) (Fig 3.7; Appendix C, Table 4.C).

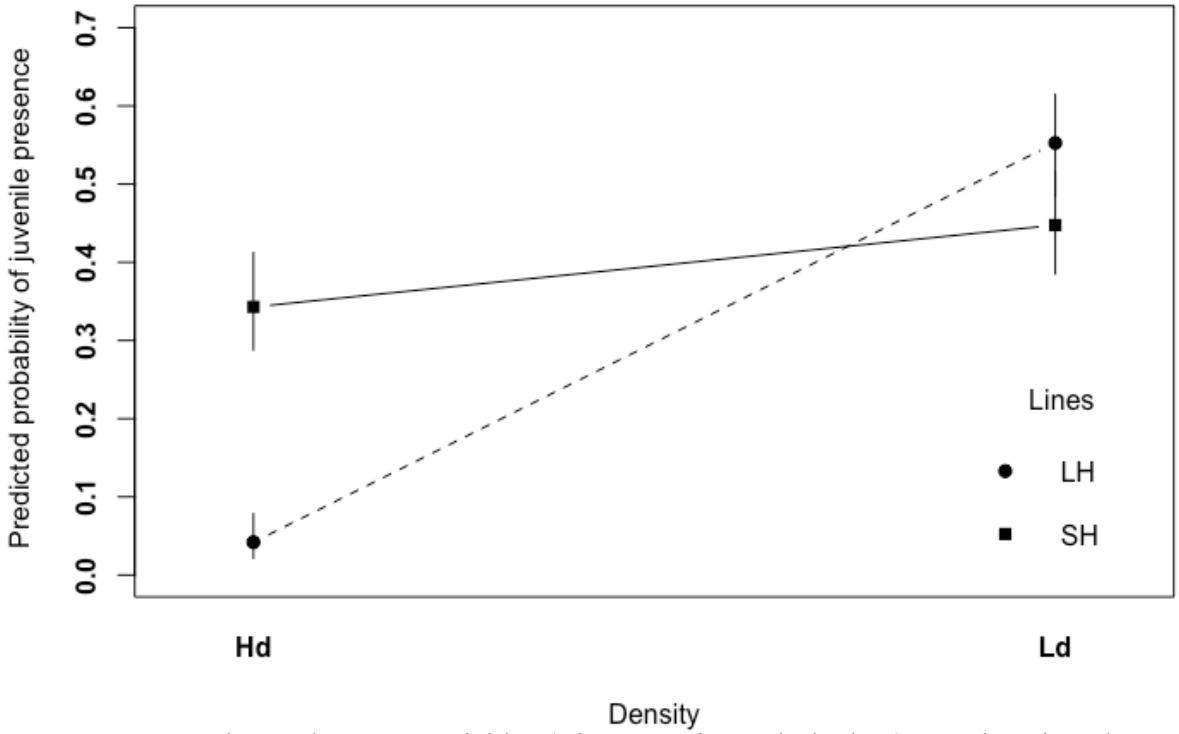

Figure 3.7: The explanatory variables (Line, Density and Shadow) tested against the probability of juvenile presence. Lines crossing the points of SH and LH represents standard error lines. Hd – high density; Ld – Low density; LH – large-size harvested; SH – small-size harvested.

Table 3.5: The summary for the generalized linear mixed model testing for the effects of explanatory variables (Density, Light and Line) on the presence of juvenile. SH – Small-size Harvested; LH – Large-size Harvested; Hd – High density; Ld – Low density; LL – Low Light; HL – High Light. Significant p-values presented in bold.

Juvenile		Chisq	Df	P-value
	Line	1.09	1	0.295
	Density	9.47	1	**0.002**
	Light	0.01	1	0.914
	Line:Density	10.31	1	**0.001**

4 Discussion

The objective of this study was to elucidate the potential effects of environmental conditions (density, primary production) on the population dynamics of two lines of medaka selected for either small or large size. The density treatment (high and low) had large impact on growth rates individual growth rates of recaptured adult fish and on the recruitment of larvae and juveniles. At low density, the growth rate of recaptured individuals were higher compared to at high density. The recruitment of both larvae and juveniles was high at the low density compared to at high density. Yet, there were only small differences in growth rate and recruitment between the two selected lines. The only differences observed between the lines was a larger number of juveniles from the large-size harvested (LH) line under high density. The light intensity treatment lead to small differences in primary production, and this did not lead to a significant effect on either growth or recruitment. Overall, density (high and low) was the treatment explaining most of the difference in growth rate and recruitment in the experiment.

4.1 size-selected lines (large-size harvested and small-size harvested)

Two lines of medaka was selected for over 10 generations on their body size (small and large) to assess the impact selective fishing can have on the population dynamic at different densities and light conditions. The marked adult fish was used to quantify for the specific growth rate in length (SGR, % $month^{-1}$) obtained during the experiment, and whether the growth rate differed between the two size-selected lines. Our findings showed little to no variation in the SGR for the marked adults between the two size-selected lines (see Fig 3.3), and that there was limited growth during the experiment (Appendix B, Table 2.B). Many larvae and juveniles was observed early in the experiment (fig 3.4), this might indicate that the adults was already actively reproducing. This means that they all are allocating the energy over to reproduction rather than somatic growth (Kozlowski, 1992; M. Heino & Kaitala, 1999). Also, if competition arise from decreasing resources, one could expect an increase in size-variation if growth is size-dependent (Peacor et al., 2007), thus the results from Figure 3.3 might indicate that competition for resources was low as there was minor variation in growth between the marked adults in the size-selected lines. Further, size-selective fishing of larger individuals can lead to the evolution of smaller body size, slower growth and earlier

maturation (Conover & Munch, 2002; Walsh et al., 2006). But the measurements was conducted on already grown individuals, and maybe the growth of juveniles could have given a different picture on the growth rate as they undergoing growth. there are several other studies showing that size-selective fishing can promote differences in growth rate (e.g. juveniles) (Hanson & Chouinard, 1992; Swain et al., 2007; Nusslé et al., 2009). Thus, the possibility that size-selective fishing can promote differences in growth rate are increasing, but to my knowledge, not many studies have used medaka (*Orzyias latipes*) in the context of size-selective fishing expect for one by Reneville (Renneville, 2016). A size-selection experiment on medaka was conducted by Renneville (2016) and found reasons to believe that size-selective fishing can promote differences in growth rates for medaka, and the medaka in this study comes from Reneville (2016). Even though the results show no difference in growth rates between the size-selected lines, something do happens in the recruitment from larvae to juvenile, possibly indicating that size-selective fishing can promote differences in recruitment for the two size-selected lines.

Body size can be correlated with reproductive effort, thus, smaller individuals can produce smaller offspring, and larger individuals might produce larger individuals with better survival (Barneche et al., 2018). The recruitment of larvae between the two size-selected lines did not show any sign of differences in recruitment (see Fig 3.6). But something happens in the transition from larvae to the recruitment of juveniles, as the recruitment of juveniles for the two size-selected lines were found to differ between each other (see Fig 3.7). The transition from larvae to juveniles can be considered as a critical period on whether they will survive to the adult stage, and factors like resources abundance might play a role on whether they will survive or die from starvation (Leggett & Deblois, 1994). This might indicate that larvae from the large-size harvested (LH) suffered more from resources depletion than larvae from the small-size harvested (SH) line in the transition to juveniles. Yet, the results of primary production shows little variations between the treatments during the experiment (see Table 3.2), assuming that resource depletion might not have been the case for the difference in juveniles observed between the selected lines. Further, the probability of detecting juveniles was 2 times higher for small-size harvested (SH) line compared to the large-size harvested (LH) line (see Table 3.5). This might reflect that continuous selection on larger fish individuals within a population can cause a truncated age and size, which can further have an effect by decreasing the recruitment (Hsieh et al., 2006).

Another most likely reason for the difference in recruitment of juveniles between the size-selected lines might be cannibalism by the adult individuals rather than resource depletion. During the observations under the experiment, on few accounts I observed adult individuals attacking either larvae or juvenile that had just came out of the larvae stage. Body size can determine the competition for resources, and larger body-size and faster growing individuals might be more bold and possibly exert to cannibalism if competition for resources are high (Post & Johnston, 1999). Thus, this might indicate that cannibalism was higher for the large-size harvested (LH) line compared to the small-size harvested (SH) line, as we observed more juveniles from small-size harvested (SH) compared to large-size harvested (LH) line during the experiment(see Fig 3.7).

4.2 Density (high density and low density)

Density dependence is crucial in population ecology, where increased density can result in a decrease in individual growth rate, reproduction and survival, and are usually determined by increased intraspecific competition for food (Myrvold & Kennedy, 2015; Gemert & Andersen, 2018). Density was used as an environmental factor to assess if the different densities had any impact on the population dynamic for growth of recaptured marked individuals and recruitment for larvae and juvenile. Here we found a significant difference of density (high and low) on specific growth rate in length for the recaptured marked individuals (see Fig 3.3). This showed that the specific growth rate in length was almost 5 times higher for the recaptured marked individuals from low density compared to those at high density (see Appendix B, Table 1.B). Thus, this might concur with the results from density on growth (see Fig 3.3) that intraspecific competition was higher for the recaptured marked individuals at high density, while intraspecific competition was low at low density.

Density did not seem to affect the survival of marked recaptured individuals, as 95% of marked individuals from start was found at the end of the experiment (see Appendix B, Table 2.B). Even if density can in reduce the individual growth rate (Jenkins Jr et al., 1999), it may take more time for competition to be the only source of mortality (Hixon & Jones, 2005). Thus, maybe the length of the experiment was not sufficient enough to observe density-dependent mortality of marked individuals, but long enough to observe that difference in density had an impact on the growth rate of marked recaptured individuals. Further, density

had great impact on the recruitment of larvae and juveniles, even showing an interaction effect with the size-selected lines.

As fisheries in most cases are based on demographic calculations, one can assume that density-dependent processes are key-regulations of recruitment in the early life (e.g. larvae and juveniles) (Andersen et al., 2017). From our results, we found great differences of recruitment for both larvae and juvenile at different densities (high and low), where observations of larvae and juveniles was highest at low density compared to high density (see Fig 3.6 and Fig 3.7). Yet, this might be unexpected as there was higher numbers of females at start in high density compared to low density, thus one would expect a higher number of larvae at high density at the start of the experiment, but the timeline (see Fig 3.4) tells a different story. Two possible scenario arises: either strong competition between females, where it was shown that zebrafish (*Danio rerio*) suppressed the reproduction of other females by using waterborn pheromones (Gerlach, 2006), or strong signs of cannibalism (Smith & Reay, 1991). Yet, less attention has been given to competition among females as males are considered the primary component in sexual selection (Gerlach, 2006). The more plausible theory might be cannibalism, as stated earlier, I observed adult fish attacking larvae and juveniles on few accounts.

To avoid cannibalism, floating wool shelters and floating plastic threads were added to provide spawning substrate and protection for larvae (see Fig 2.4). Yet, the results from larvae (see Fig 3.6) suggest that cannibalism was high at high density compared to low density. Interesting is that of juveniles, as the two-size selected lines differed in their observation at high density (interaction of lines and density), where small-size harvested (SH) line showed higher abundance of juveniles compared to large-size harvested (LH) line (see Fig 3.7). This might indicate that large-size harvested (LH) line is more cannibalistic than small-size harvested (SH) line at high density. As growth showed no difference in body size (see Fig 3.3), possible explanation of cannibalism might be shown in the behavior of the adult fish (Hecht & Pienaar, 1993), possibly showing that large-size harvested (LH) line expressed a more aggressive behavior than small-size harvested (SH) line. Further, both larvae and juveniles was most abundant at low density (see Fig 3.6 and Fig 3.7) throughout the experiment, indicating low competition and low cannibalism.

4.3Light condition (High light and low light; primary production)

Two different types of light condition was used to assess if difference in primary production affected the growth of recaptured marked individuals, and the recruitment of larvae and juveniles for the two size-selected lines. The results from the light condition (high and low) showed no significant effect on the growth rate for recaptured marked individuals (see Fig 3.3), neither did it show any significant effect on the recruitment of larvae and juveniles (see Fig 3.6 and Fig 3.7). Yet, variation in chlorophyll-a concentration (see Fig 3.2) was found, but it did not significantly vary over time. The answer might be in ecosystem processes, as it indicates the extent of trophic-structure responses to selective fishing (Shepard et al., 2012), but analyzes of ecosystem processes was not conducted for this study. Another theory is that bottom-up effects are masked by top-down effects, as light might also exert a top-down effect as it is important for visual search of resources in many fish (Aksnes et al., 2004). Even so, analyzes on ecosystem processes, and how the two size-selected line impact the ecosystem, might give a more clear answer on how the two different light conditions might affects the growth and recruitment than just primary production changes over time.

4.4 Evaluating potential "errors"

Visual observations of a size-structured population (adult, juveniles and larvae) can be difficult, especially if fish are small. The experiment was conducted outdoors on a large field and exposed to all kinds of weather (rain, sunlight, wind etc.) which could affect the visual observation during the experiment (e.g. wind and rain breaking the water surface). But three replicated observations per mesocosm was conducted to increase the possibility of observing individuals (adult, juveniles and larvae) during the experiment.

Some mesocosms had high turbidity making it difficult to observe the individuals, thus the possibility of wrongful observation of individuals might increase for the mesocosms with high turbidity. One possibility might have been to include the observation of high turbidity in the study, thus possibly "correcting" for the numbers of individual observed in the mesocosm.

The most realistic error might be the classification of larvae and juveniles. Adults was easily distinguished from the larvae and juveniles, but distinguishing between larvae and early stage juvenile was sometimes a challenge. Distinguishing between larvae and juveniles was based on length range (in mm), and the knowledge of larvae and juveniles being closer to the water surface while adults usually residing at the mid-to-bottom of the mesocosms. Thus, on few occasions, some early stage juveniles might have been mistaken as larvae, thus the juveniles might have been present earlier on in the experiment than first thought (see Fig 3.5).

5 Conclusion

In conclusion, the environmental conditions (density and light) differed in their impact on the growth rate of marked adult fish and recruitment of larvae and juveniles for the two size-selected lines. The two-size selected lines showed very little difference in growth rate of the marked adult fish and the recruitment of larvae, only difference between the lines was found at the juvenile stage. Density was the environmental condition with the largest impact on growth rate and recruitment, while light conditions had no impact on the growth rate or the recruitment.

The size-selected lines of medaka did not show any great differences in growth rate of the marked adult fish, neither for the recruitment of larvae. Yet, variation was found at the juvenile stage, were presence of juvenile was higher for small-size harvested line compared to large-size harvested line. This can indicate to some degree that selective fishing can cause an impact in the recruitment of juveniles.

Density had the clearest effect on growth rate of marked adult fish and recruitment of larvae and juveniles. Yet, differences in density did not seem to have any divergent effects of growth rate for the two size-selected lines, neither did it show any differences in recruitment for the two size-selected lines. But differences in density was shown to impact the recruitment of juveniles for the two size-selected lines, possibly indicating that environmental conditions (density) can further have implications for the changes in population dynamics caused by selective fishing.

Light, shown as high light (HL) attenuation and low light (LL) attenuation did not have any impact on the growth rate for marked adult fish and recruitment of larvae and juveniles. The use of primary production alone might not have been sufficient enough to find any effects, possibly adding zooplankton measurements might have given a different answer, but it was not implemented in this study.

Overall, density had the highest impact on the population dynamic, while light showed no effects. The size-selection did not show any differences in growth rate, but did shown differences at the juvenile stage, possibly indicating that size-selective fishing can alter the

population dynamics of harvested population. Future studies may cast light over the effects that size-selective fishing can have on population dynamics. As density had the clearest effect on growth rate and recruitment, I would suggest implementing ecosystem processes to further analyze if size-selective fishing might alter the population composition, to get a better understanding on how size-selective fishing might impact fish populations.

References

Aksnes, D. L., Nejstgaard, J., Sædberg, E., & Sørnes, T. (2004). Optical control of fish and zooplankton populations. *Limnology and Oceanography, 49*(1), 233 - 238.

Allendorf, F. W., England, P. R., Luikart, G., Ritchie, P. A., & Ryman, N. (2008). Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution, 23*(6), 327 - 337.

Andersen, K. H., Jacobsen, N. S., Jansen, T., & Beyer, J. (2017). When in life does density dependence occur in fish populations? *Fish and Fisheries, 18*(4), 656 - 667.

Audzijonyte, A., Fulton, E. A., & Kuparinen, A. (2015). The impacts of fish body size changes on stock recovery: a case study using an Australian marine ecosystem model. *ICES Journal of Marine Science, 72*(3), 782 - 792.

Audzijonyte, A., Kuparinen, A., & Fulton, E. A. (2013). How fast is fisheries-induced evolution? Quantitative analysis of modelling and emperical studies. *Evolutionary Applications, 6*(4), 585 - 595.

Baras, E., & Jobling, M. (2002). Dynamic of intracohort cannibalism in cultured fish. *Aquaculture Research, 33*(7), 461 - 479.

Barneche, D. R., Roberstion, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science, 360*(6389), 642 - 645.

Barton, B. A., & Iwama, G. K. (1991). Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. *Annual Review of Fish Diseases, 1*, 3 - 26.

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.42.1. Retrieved from https://cran.r-project.org/package=MuMIn

Bates, D., Machler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1 - 48. doi:10.18637/jss.v067.i01

Beamish, R. J., McFarlane, G. A., & Benson, A. (2006). Longevity overfishing. *Progress in Oceanography, 68*(2-4), 289 - 302.

Birkeland, C., & Dayton, P. K. (2005). The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution, 20*(7), 356 - 358.

Biro, P. A., & Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the national academy of Sciences, 105*(8), 2919 - 2922.

Biro, P. A., & Sampson, P. (2015). Fishing directly selects on growth rate via behaviour: implications of growth-selection that is independent of size. *Proceedings of The Royal Society B: Biological Sciences, 282*(1802), 1 - 6.

Breen, M., Graham, N., Pol, M., He, P., Reid, D., & Suuronen, P. (2016). Selective fishing and balanced harvesting *Fisheries Research, 184*, 2 - 8.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accerelared modern human-induced species losses: Entering the sixth mass extinction. *Science Advances, 1*(5), 1 - 5.

Chapin III, S. F., Zavaleta, S. E., Eviner, T. V., Naylor, L. R., Vitousek, M. P., Reynolds, L. H., . . . Díaz, S. (2000). Consequences of changing biodiversity. *Nature, 405*, 234 - 242.

Clark, W. (1976). The lessons of the Peruvian anchoveta fisheri. *California Cooperative Oceanic Fisheries Investigations Reports, 19*, 57 - 63.

Conover, O. D., & Munch, B. S. (2002). Sustaining Fisheries Yields Over Evolutionary Time Scales. *Science, 297*, 94 - 96.

Crawley, M. J. (2007). *The R Book*. Chichester, West Sussex, United Kingdom: Wiley.

De Roos, A. M., & Persson, L. (2002). Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the national academy of Sciences, 99*(20), 12907 - 12912.

Dickerson, B. R., Brinck, K. W., Willson, M. F., Bentzen, P., & Quinn, T. P. (2005). Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology, 86*(2), 347 - 352.

Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and boss. *Annual Review of Environment and Resources, 28*, 137 - 167.

Edeline, E. (2016). Life-History Evolution, Human Impacts on. *Encyclopedia of Evolutionary Biology, 2*, 335 - 342.

Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology, 17*(1), 209-220.

Fisher, J. A. D., Frank, K. T., & Leggett, W. C. (2010). Global variation in marine fish body size and its role in biodiversity - ecosystem functioning. *Marine Ecology, 405*, 1 - 13.

Fryxell, D. C., Arnett, H. A., Apgar, T. M., Kinnison, M. T., & Palkovacs, E. P. (2015). Sex ratio variation shapes the ecological effects of a globally introduced freshwater fish. *Proceedings of The Royal Society B: Biological Sciences, 282*(1817), 1 - 8.

Garcia, S. M., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., Arimoto, T., . . . Smith, A. D. M. (2012). Reconsidering the Consequences of Selective Fisheries. *Science, 335*(6072), 1045 - 1047.

Gemert, R. V., & Andersen, K. H. (2018). Implications of late-in-life density-depedent growth for fishery size-at-entry leading to maximum sustainable yield. *ICES Journal of Marine Science, 75*(4), 1296 - 1305.

Gerlach, G. (2006). Pheromonal regulation of reproductive success in female zebrafish: female suppression and male enhancement. *Animal Behaviour, 72*(5), 1119 - 1124.

Hanson, J. M., & Chouinard, G. A. (1992). Evidence that size-selective mortality affects growth of Atlantic cod (*Gadus morhua L.*) in the southern Gulf of St Lawrence. *Journal of Fish Biology, 41*(1), 31 - 41.

Hartig, F. (2018). *DHARMa: Residual Diagnostics for Hierarchial (Multi-level / Mixed) Regression Models*.

Hecht, T., & Pienaar, A. G. (1993). A review of Cannibalism and its Implications in Fish Larviculture. *Journal of World Aquaculture Society, 24*(2), 246 - 261.

Heino, M., & Godø, O. R. (2002). Fisheries-induced Selection Pressures in the Context of Sustainable Fisheries. *Bulletin of Marine Science, 70*(2), 639 - 658.

Heino, M., & Kaitala, V. (1999). Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology, 12*, 423 - 429.

Heino, M., Pauli, B. D., & Dieckmann, U. (2015). Fisheries-Induced Evolution. *Annual Review of Ecology, Evolution, and Systematics, 46*(1), 461-480. doi:10.1146/annurev-ecolsys-112414-054339

Hixon, M. A., & Jones, G. P. (2005). Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology, 86*(11), 2847 - 2859.

Hsieh, C., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., & Suighara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature, 443*, 859 - 862.

Hutchings, J. A., & Myers, R. A. (1994). What can be learned from the Collapse of Renewable Resource? Atlantic Cod, Gadus morhua, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences, 51*(9), 2126 - 2146.

Iwamatsu, T. (2004). Stages of normal development in the medaka Oryzias latipes. *Elsevier, 121*(7-8), 605 - 618.

Jenkins Jr, T. M., Diehl, S., Kratz, K. W., & Cooper, S. D. (1999). Effect of population density on individual growth of brown trout in streams. *Ecology, 80*(3), 941 - 956.

Jobling, M. (1983). Growth studies with fish-overcoming the problems of size variation. *Journal of Fish Biology, 22*(2), 153 - 157.

Jørgensen, C., Ernande, B., & Fiksen, Ø. (2009). Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evolutionary Applications, 2*(3), 356 - 370.

Jørgensen, C., & Fiksen, Ø. (2010). Modelling fishing-induced adaptations and consequences for natural mortality. *Canadian Journal of Fisheries and Aquatic Sciences, 67*(7), 1086 - 1097.

Kinoshita, M., Murata, K., Naruse, K., & Tanaka, M. (2009). *Medaka: Biology, Management, and Experimental Protocols*: Wiley-Blackwell.

Kozlowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology & Evolution, 7*(1), 15 - 19.

Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution, 22*(12), 652 - 659.

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science, 57*(3), 659 - 668.

Leflaive, J., Danger, M., Lacroix, G., Lyautey, E., Oumarou, C., & Ten-Hage, L. (2008). Nutrient effects on the genetic and functional diversity of aquatic bacterial communities. *Fems - Microbiology ecology, 66*(2), 379 - 390.

Leggett, W. C., & Deblois, E. (1994). Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research, 32*(2), 1994.

Longhurst, A. (2002). Murphy´s law revisited: longevity as a factor in recruitment to fish populations. *Fisheries Research, 56*(2), 125-131.

Lorenzen, K., & Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the royal Society B: Biological Sciences, 269*(1486), 49 - 54.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature, 423*, 280-283.

Myrvold, K. M., & Kennedy, B. P. (2015). Density dependence and its impact on individual growth rates in an age-structured stream salmonid population. *Ecosphere, 6*(12), 1 - 16.

Nakagawa, S., & Schielzeth, H. (2012). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133-142.

Nusslé, S., Bornand, C. N., & Wedekind, C. (2009). Fishery-induced selection on an Alpine whitefish: quantifying gentic and environmental effects on individual growth rate. *Evolutionary Applications, 2*(2), 200 - 208.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres Jr, F. (1998). Fishing Down Marine Food Webs. *Science, 279*(5352), 860 - 863.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, R., Walters, C. J., . . . Zeller, D. (2002). Towards sustainability in world fisheries. *Nature, 418*, 689 - 695.

Peacor, S. D., Bence, J. R., & Pfister, C. A. (2007). The effect of size-dependent growth and environmental factors on animal size variability. *Theoretical Population Biology, 71*(80 - 94).

Post, J. R., & Johnston, N. T. (1999). Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiment. *Ecologial Monographs, 69*(2), 155 - 175.

Radovich, J. (1982). The Collapse of the California Sardine Fishery. What Have We Learned? *California Cooperative Oceanic Fisheries Investigations Reports, 23*, 56 - 78.

Renneville, C. (2016). Réponse à la sélection taille-dépendante anthropique et ses conséquences écologiques (Thèse de doctorat en Écologie). 1 - 226.

Rjinsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., & Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science, 7*(1), 1570 - 1583.

Rstudio Team. (2016). Rstudio: Integrated Development Environment for R. Boston, MA: Rstudio, Inc. Retrieved from http://www.rstudio.com/

Russell, L. (2018). Estimated Marginal Means, aka Least-Squares Means. R package version 1.2.4. Retrieved from http://cran.r-project.org/package=emmeans

Sadovy, Y. (2001). The threat of fishing to highly fecund fishes. *Journal of Fish Biology, 59*(sA), 90 - 108.

Schackell, N. L., Frank, K. T., Fisher, J. A. D., Petrie, B., & Leggett, W. C. (2010). Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of The Royal Society B: Bioloigcal Sciences, 277*(1686), 1353 - 1360.

Sharpe, D. M. T., & Hendry, A. P. (2009). Synthesis: life history changes in comercially exploited fish stocks: an analysis of trends across studies. *Evolutionary Applications, 2*(3), 260 - 275.

Shepard, S., Fung, T., Houle, J. E., Farnsworth, K. D., Reid, D. G., & Rossberg, A. G. (2012). Size-selective fishing drives species composition in the Celtic Sea. *ICES Journal of Marine Science, 69*(2), 223 - 234.

Smith, C., & Reay, P. (1991). Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries, 1*(1), 41 - 64.

Swain, D. P., Sinclair, A. F., & Hanson, J. M. (2007). Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the royal Society B: Biological Sciences, 274*(1613), 1015 - 1022.

Tonn, W. M., Holopainen, I. J., & Paszkowski, C. A. (1994). Density-Depedent Effects and the regulation of Crucian Carp Populations in Single-Species Ponds. *Ecology, 75*(3), 824 - 834.

Walsh, M. R., Munch, S. B., Chiba, S., & Conover, D. O. (2006). Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letter, 9*(2), 142 - 148.

Appendix A

Estimates and means for temperature (^{o}C) and chlorophyll-a concentration (µg/L^{-1}).

Table 1.A: The estimates for the linear model used to test for the temperature (^{o}C) variation among blocks (A. B. C. D. F). and for variation of temperature (^{o}C) between blocks at different sampling events (T0-T6). Significant p-values are in bold.

Predictors	Estimate	Std.Error	t-value	P-value
Intercept	28.169	0.169	166.639	**<. 0.0001**
Block B	0.038	0.239	0.160	0.873
Block C	0.059	0.253	0.233	0.816
Block D	0.396	0.239	1.656	0.099
Block F	0.592	0.239	2.474	**0.013**

Table 2.A: Mean temperature (^{o}C) and standard deviation (SD) measured for each block over the sampling period from T0 (19.06.17) to T6 (18.09.17). (**T0** – 19.06.17; **T1** – 10.07.17; **T2** – 24.07.17; **T3** – 08.08.17; **T4** – 21.08.17; **T5** – 04.09.17; **T6** – 18.09.17).

Block	T0 mean (SD)	T1 Mean (SD)	T2 mean (SD)	T3 mean (SD)	T4 mean (SD)	T5 mean (SD)	T6 mean (SD)
A	28.12 (0.74)	23.19 (0.33)	18.74 (0.36)	21.15 (0.30)	21.03 (0.48)	20.68 (0.98)	12.80 (0.39)
B	28.20 (0.29)	23.15 (0.26)	18.65 (0.24)	21.08 (0.23)	20.85 (0.29)	20.82 (0.43)	13.01 (0.25)
C	28.27 (0.69)	23.02 (0.30)	18.60 (0.15)	21.15 (0.19)	21.03 (0.46)	21.04 (0.70)	13.22 (0.49)
D	28.49 (0.95)	23.25 (0.23)	18.67 (0.18)	21.27 (0.24)	21.51 (1.08)	21.32 (1.07)	13.62 (0.70)
F	28.86 (0.74)	23.18 (0.20)	18.74 (0.29)	21.34 (0.21)	21.61 (0.54)	21.57 (0.79)	13.72 (0.39)

Table 3.A: Chlorophyll-a concentration ($\mu g/L^{-1}$) in mean and standard deviation measured for each treatment over the sampling period from T0 (19.06.17) to T6 (18.09.17)). SH – Small-size harvested; LH – Large-size harvested; Hd – High density; Ld – Low density: LL – Low light; HL – High light.

Treatment	T0 mean (SD)	T1 Mean (SD)	T2 mean (SD)	T3 mean (SD)	T4 mean (SD)	T5 mean (SD)	T6 mean (SD)
SH-Hd-LL	1.80 (1.37)	5.28 (2.22)	7.04 (3.63)	5.61 (3.05)	4.27 (3.38)	9.25 (5.78)	5.05 (3.63)
SH-Hd-HL	2.89 (0.57)	6.63 (2.80)	4.15 (1.39)	7.08 (1.99)	6.02 (3.15)	4.82 (3.36)	1.42 (1.98)
SH-Ld-LL	2.92 (0.87)	3.66 (1.80)	3.93 (2.66)	6.08 (2.87)	5.28 (2.96)	6.10 (5.21)	2.46 (3.13)
SH-Ld-HL	3.13 (1.15)	6.01 (2.69)	5.23 (3.64)	4.69 (3.67)	5.99 (5.48)	5 (4.49)	1.20 (1.80)
LH-Hd-LL	2.70 (1.24)	7.43 (2.51)	7.12 (3.13)	7.56 (3.41)	6.73 (3.42)	9.35 (3.32)	3.79 (2.01)
LH-Hd-HL	3.04 (1.75)	12.32 (5.69)	5.05 (2.01)	10.73 (8.08)	12.80 (9.48)	8.78 (5.95)	3.97 (5.11)
LH-Ld-LL	4.1 (2.34)	3.95 (2.34)	7.12 (5.19)	5.64 (4.39)	4.26 (2.17)	4.46 (3.03)	1.20 (1.16)
LH-Ld-HL	2.64 (1.41)	7.10 (3.37)	4.45 (1.54)	9.29 (7.65)	4.20 (4.80)	5.38 (6.27)	2.99 (4.28)

Appendix B

Number of recaptured marked individuals and estimations for the specific growth rate for length in mm (SGR, % month^{-1})

Table 1.B: Estimates for the linear model used to test for the specific growth rate for length in mm (SGR, % month^{-1}) of the recaptured marked individuals for line (SH and LH), density (Hd and Ld) and light (HL and LL). Significant P-values are represented in bold.

SGR % month^{-1}	Estimate	Std.Error	t-value	P-value
Intercept	7.92	0.27	28.58	**<0.001**
LineSH	-0.39	0.31	-1.27	0.204
DensityLD	4.76	0.38	12.51	**<0.001**
LightLL	-0.00	0.31	-0.02	0.978

Table 2.B: Number of tagged fish initially released in the mesocosm (n = 360) and recaptured at the end of the experiment. Distribution of individuals used for the different treatments (Line – SH and LH; Density – Hd and Ld; light – HL and LL).

Treatments	Nb. of tagged fish at the beginning of the experiment	Nb. of recaptured fish at the end of the experiment	Mean initial length (mm) at the beginning of the experiment	Mean final length (mm) at the end of the experiment
Small-size harvested (SH)	180	168	19.43	25.05
Large-size harvested (LH)	180	171	18.91	24.65
High density (Hd)	288	269	19.09	24.23
Low density (Ld)	72	70	19.5	28.49
High light (HL)	180	172	19.03	24.63
Low light (LL)	180	167	19.31	25.09
Total	360	339		

Appendix C

estimates for larvae and juveniles per sampling event (T0 – T4) and presence/absence.

Table 1.C: The estimates of the linear model used to test for the effects of Line, density and light on number of larvae. Significant p-values are represented in bold. (Line, SH- small-size harvested; LH – large-size harvested, Density, Hd – high Density; Ld – low density and Light, HL – high light; LL – low light)).

Larvae (T0)		Estimates	Std.Error	Z-value	P-value
	Intercept	0.36	0.36	0.98	0.324
	LineSH	1.60	0.42	3.75	**<0.001**
	DensityLd	2.30	0.42	5.47	**<0.001**
	LightLL	0.08	0.27	0.30	0.762
	LineSH:DensityLd	-1.67	0.55	-2.99	**0.002**
(T1)					
	Intercept	0.18	0.40	0.46	0.643
	LineSH	1.26	0.47	2.67	**0.007**
	DensityLd	2.44	0.45	5.31	**<0.001**
	LightLL	0.17	0.29	0.57	0.563
	LineSH:DensityLd	-1.11	0.61	-1.82	0.067
(T2)					
	Intercept	-0.62	0.38	-1.60	0.109
	DensityLd	2.18	0.31	6.87	**<0.001**
	LineSH	0.58	0.40	1.45	0.145
	LightLL	0.66	0.40	1.66	0.096
	LineSH:LightLL	-1.12	0.56	-1.98	**0.046**
(T3)					
	Intercept	-1.20	0.43	-2.77	**0.005**
	LineSH	0.29	0.32	0.90	0.367
	DensityLd	2.30	0.39	5.90	**<0.001**
	LightLL	0.45	0.32	1.38	0.165
(T4)					
	Intercept	-2.10	0.68	-3.07	**0.002**
	DenstyLd	2.02	0.42	4.2	**<0.001**
	LineSH	1.30	0.71	1.83	0.066
	LightLL	1.68	0.69	2.41	**0.015**
	LineSH:LightLL	-1.57	0.92	-1.71	0.086

Table 2.C: The estimates of the linear model used to test for the effects of Line, density and light on number of juveniles. Significant p-values are represented in bold. (Line, SH- small-size harvested; LH – large-size harvested, Density, Hd – high Density; Ld – low density and Light, HL – high light; LL – low light).

Juvenile (T2)		Estimate	Std.Error	Z-value	P-value
	Intercept	-1.80	0.75	-2.438	**0.017**
	LineSH	2.60	0.79	3.27	**0.001**
	DensityLd	3.25	0.78	4.15	**<0.001**
	LightLL	0.01	0.29	0.06	0.950
	LineSH:DensityLd	-2.31	0.87	-2.65	**0.007**
(T3)					
	Intercept	-1.96	0.71	-2.75	**0.005**
	LineSH	3.12	0.78	3.97	**<0.001**
	DensityLd	3.05	0.68	4.46	**<0.001**
	LightLL	0.90	0.48	1.85	0.063
	LineSH:DensityLd	-2.22	0.77	-2.86	**0.004**
	LineSH:LightLL	-1.14	0.60	-1.18	0.059
(T4)					
	Intercept	-2.90	1.06	-2.72	**0.006**
	LineSH	4.02	1.10	3.62	**0.001**
	DensityLd	3.96	1.04	3.77	**0.001**
	LightLL	0.70	0.46	1.53	0.124
	LineSH:DensityLd	-3.20	1.10	-2.90	**0.003**
	LineSH:LightLL	-1.07	0.57	-1.88	0.059

Table 3.C: Estimates for the generalized linear mixed model used to test the effects of explanatory variables (Density, Light and Line) on the presence of larvae. SH – Small-size harvested; LH – large-size harvested; Hd- High density; Ld – low density; HL – high light; LL – low light. Significant P-values are represented in bold.

Larvae		Estimate	Std.Error	Z-value	P-value
	Intercept	-0.06	0.70	-0.08	0.930
	LineSH	0.09	0.75	0.12	0.903
	DensityLD	2.92	0.86	3.39	**<0.001**
	LightLL	0.09	0.75	0.12	0.901

Table 4.C: The estimates for the generalized linear mixed model testing for the effects of explanatory variables (Density, Light and Line) on the presence of juvenile. SH – Small-size Harvested; LH – Large-size Harvested; Hd – High density; Ld – Low density; LL – Low Light; HL – High Light. Significant p-values presented in bold.

Juvenile		Estimate	Std.Error	Z-value	P-value
	Intercept	-3.28	0.74	-4.38	**<0.001**
	LineSH	2.53	0.77	3.27	**0.001**
	DensityLd	3.47	0.79	4.37	**<0.001**
	LightLL	0.04	0.39	0.10	0.914
Post-hoc test on interaction for juvenile					
		Estimate	**SE**	**Z-ratio**	**P-value**
	LH,Hd – SH, Hd	-2.54	0.77	-3.26	**0.005**
	LH,Ld – SH,Ld	0.45	0.50	0.90	0.802