The Evolutionary Effects of Fishing: Implications for Stock Management and Rebuilding

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Recent empirical studies have demonstrated inter-generational morphological and life-history changes in fish stocks that have been impacted by size-selective harvest. Evolutionary processes in biological populations occur through differential survival and reproductive success based, in part, upon individual phenotypic variability. Fishing is a source of directional selection resulting in the directed removal of some phenotypes; however, many aspects of the evolutionary effects of fishing remain have yet to be described. In order to better understand the life-history and morphological changes that occur as a result of size-selective fishing, and their effect on fishery dynamics, I first determined the suitability of Japanese medaka (Oryzias latipes) for selection experiments. I performed selection experiments using Japanese medaka and report how morphology and life-history characteristics changed over multiple generations of selection. I then used these patterns of change in life-history and morphology to validate individual-based simulation candidate models to test general mechanisms of life-history relationships. Finally, I applied the individual-based simulation modeling approach in order to describe how biological and fishery characteristics change in a large, age-structured population exposed to size-selective fishing over multiple generations. I found that the Japanese medaka has attractive characteristics for biological investigation. The selection experiments indicated large changes in the age-at-maturity, including a nearly 50% decrease over four generations in the most intense size-selective removal regimes. However, I did not observe significant changes in length-at-age or weight-at-age over the course of the experiment. Candidate simulation models were poor at
predicting some aspects of the life-history characteristics of Japanese medaka. The simulation model to determine fishery characteristics predicted large decreases in yield and egg production as a result of decreases in length-at-age. Understanding the relationships of life-history characteristics and their role in determining population resilience is a step toward understanding the importance of evolutionary processes in fishery management.
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Introduction: Demographic, Quantitative Genetic and Life-history Aspects of Fishery-Induced Evolution

In this chapter, I review aspects of demography, quantitative genetics, and life-history theory relevant to fishery-induced evolution (FIE). The goal of this work is the reconciliation of these disparate branches of the biological sciences into a conceptual framework relevant to the goals of natural resource management. The initiation of this study was motivated by recent works that have demonstrated a decline in the abundance of fished populations and a lack of population recovery following periods of fishing moratoria (Hutchings 2005). These pioneering works have described changes in morphology and life history of fished stocks over decadal time periods (Ricker 1981, Olsen et al. 2005, Haugen et al. 2008). These studies indicate that fished stocks may not be as resilient as previously assumed and that changes in the nature of the stock may obviate the role of compensatory ecological mechanisms (Myers et al. 1995, Shelton and Healey 1999, Bowers and White 2002). In many instances, a suite of factors contribute to a lack of population recovery: ecosystem changes, population level depensatory mechanisms, and evolutionary (Chouinard 2002).

Phenotypic variability and life-history theory

Evolutionary processes in biological populations, such as FIE, occur as a result of differential survival and reproductive success (natural selection) that is based upon individual phenotypic variability (Darwin 1859). Fisher’s (1930) fundamental theory of evolution implies that those traits most important to fitness will be conserved through evolution and will have low variability within a population (Frank and Slatkin 1992). However, it is rare that phenotypic traits are fixed
in populations (de Jong 1990), and fitness-related traits can be variable (Houle 1992). Fishes in
particular display a great amount of intra-specific morphological (phenotypic) variability relative
to other vertebrates (Mayr 1969, Allendorf et al. 1987). Sources of phenotypic variability include
environmentally influenced phenotypic plasticity (independent of genotype) as well as
genetically derived variability: both sources of variation will influence the range of phenotypes
exhibited among individuals. Genetic differences among individuals occur as a result of
mutation, recombination, and other historical circumstances and this variability is conserved, in
the face of selection, because of the complexity of the environment in space and its temporally
stochastic nature. The components of phenotype that determine the schedules of ontogenetic
events such as the timing of sexual development, rates of somatic and sexual development, and
mortality schedules are referred to as an organism’s life-history pattern and can vary as a result
of genetic differences among individuals as well as environmental factors (Roff 2002).

Patterns of life history are determined by the dynamic allocation of energy through ontogeny
for growth, survival, and reproduction. The differences among individuals in these traits reflect
alternative strategies to maximize reproductive output. The Euler-Lotka equation describes the
expected lifetime production of female offspring, \( R_0 \) in a stationary population (Roff 2002):

\[
R_0 = \sum_{x=0}^{\infty} l_x m_x ,
\]

where the value of \( l_x \) is the probability of survival of an age \( x \) individual and \( m_x \) is the age-
specific production of female offspring. The structure of the Euler-Lotka equation allows many
ways by which \( R_0 \) can be maximized by varying the relative values of age-specific effects
(Kozlowski and Wiegert 1986, Parker and Smith 1990).

The transfer of genetic information from parents to offspring is the mechanism responsible
for defining the genetic component of phenotypic similarity between generations of related
individuals. Phenotypic characteristics, such as the life-history characteristics described above, are continuous traits that are controlled by complex genetic, environmental, and interactive (genetic × environmental) processes (Lynch and Walsh 1998). Individuals that are best able to optimize survival and reproduction maximize their reproductive output and produce offspring whose genetic composition is similar to their own. Thus, it is these genetic components contributing to fitness that become prevalent in the population over generations. It generally is not possible to describe how genetic information is translated into phenotypic characteristics by sampling at the molecular level (Reed and Frankham 2001), but a variety of quantitative genetic protocols are available to predict how morphological and life-history patterns change as the result of phenotype-based selective processes (Falconer 1986, Hallerman 2003).

**Evolution of phenotypic traits**

Evolution may be defined as the change in phenotype as a result of selective processes, as opposed to variation that is a result of expression of the range of potential phenotypes (phenotypic plasticity). There are three necessary conditions for phenotypic trait evolution to occur (Roff 1997). The first requirement is that there is genetic variation controlling the expression of the trait(s) under examination. The genetic variance of a trait can be partitioned into components. The additive component of genetic variance \( V_a \) affects the phenotype without the interaction of alleles and the non-additive component of variance affects phenotype by interaction of alleles within and across loci. For the purposes of assessing evolutionary change, \( V_a \) is the quantity of interest because the frequencies of alleles in a population will be a result of selective processes, and will be transmitted intact to succeeding generations. If the genetic variation in the population is great, there will be greater individual variation at the locus relative
to that for a population with few alleles. If genetic variation exists, then there can be a response to selection (the trait is evolvable) as a result of altering allele composition. Such a change in allele frequencies will result in corresponding phenotypic changes.

The second requirement for trait evolution to occur is selective force acting on the phenotypes. In this context, four types of selection may act on populations: stabilizing, disruptive, directional and frequency-dependent. Each type of selective process will retain or remove individuals from a population that share single phenotypes or sets of phenotypes in a population and will indirectly control the composition of genotypes among breeding individuals. Because of demographic considerations that serve to maintain fishery sustainability, regulations often target the largest individuals in a population. By subjecting large fish to greater harvest mortality, the life-history attributes of these members of the population are removed (Policansky 1981). Such selective forcing has been termed “phenotype-based selection” (Coltman et al. 2003) and results in the systematic removal of segments of the population that share similar phenotypes. Size-selective rates of fishing mortality can be intense in commercial fisheries. Ricker (1981) estimated that 80% of two-year-old pink salmon are harvested each year by the fishery. Instantaneous fishing mortality exceeds 1.0 y⁻¹ for many fish stocks, and by the nature of the gear used, this fishing is size-selective. Worldwide, estimates of fishing pressure for stocks of the families Engraulidae, Sciaenidae, Bothidae, and Pleuronectidae exceed instantaneous fishing mortality of 1.0 y⁻¹ (Mertz and Myers 1998). Such intense selection imposes a de facto selective breeding program on the remainder of the population: those individuals that remain in the population will have greater relative fitness than those harvested in the fishery.

The final necessary condition for trait evolution to occur is that the trait must be heritable. Heritability is an index that indicates the degree of resemblance of offspring to parents and
ranges from zero to one. Because information is transferred between generations through genetic mechanisms, heritability defines the degree to which a trait is under genetic control, such that when heritability approaches zero the trait is influenced only by environmental effects. Generally, the measurement of heritability ($h^2$) is defined as the ratio of the additive genetic variance to the total phenotypic variance (Roff 1997), where the total phenotypic variability is defined as $V_p$:

$$h^2 = \frac{V_a}{V_p}.$$

This estimate of heritability is termed “heritability in the narrow sense” because it does not include genetic effects from dominance and epistatic interactions (non-additive effects within and between loci, respectively) (Falconer and Mackay 1996). Heritability values for morphological and life-historical traits for wild marine fish populations are difficult to estimate because of environmental variability, overlapping generations, and long generation times. One such attempt to measure heritability made use of the philopatry of anadromous Atlantic salmon (*Salmo salar*). Jónasson et al. (1997) released 247,272 tagged smolts of four cohorts in Iceland. The heritability estimates for body weight of grilse (individuals that return after one year at sea) ranged from 0.19 to 0.36. Heritability estimates for morphological, behavioral, and life-history traits observed in the laboratory are generally non-zero (Stokes and Law 2000) and may provide reliable estimates of the magnitude and direction of heritability expressed in the field (Weigensberg and Roff 1996). Experiments upon wild populations of guppies (*Poecilia reticulata*) subjected to directional selection similar in magnitude to that observed in nature exhibited rates of evolution of age- and size-at-maturity similar to those found in artificial selection experiments in laboratory settings (Reznick and Ghalambor 2005). However, Roff
(1997) suggested that laboratory-derived values of heritability generally are positively biased because of the reduced value of phenotypic variance, $V_p$.

Given the necessary conditions for evolution of a trait to occur – variation, selection differential, and heritability – it is possible to determine how each factor will interact to determine the phenotypic response of the trait to selection over generations. The change in the mean value of a phenotypic trait between parents and offspring over generations as a result of selection is termed the “response to selection” and calculated as:

$$\Delta \mu = \mu_p - \mu_o,$$

where $\mu_p$ is the mean trait value of the parents and $\mu_o$ is the mean trait value of the offspring. The response of the trait value to the selective process has been described using the ‘breeders equation’ (Falconer 1986):

$$\Delta \mu = Sh^2,$$

where the value of $S$ is defined as the among-generation difference for the trait (the mean of entire population prior to selection and the mean of the trait value after selection). Hence, the response to selection is contingent on the magnitude of selection ($S$) and the value of heritability, $h^2$. This fundamental relationship of quantitative genetics is attributed to Pearson (Lynch and Walsh 1998) and is used in analysis of quantitative traits in both wild and captive populations.

Historically, the study of evolution has focused on causes of population differentiation and mechanisms of speciation over evolutionary timescales. Evolutionary processes occurring over short time spans (on the scale of a human lifetime) are referred to as ‘contemporary evolution’ (Ashley et al. 2003, Stockwell et al. 2003). Its description has added to understanding of the rapidity of evolutionary processes, the strength of selective forces needed to effect such changes, and the prevalence of such phenomenon. This is especially relevant to FIE, which has been
described in a variety of marine and freshwater systems. The effects of size-selective harvest previously were thought to be limited to the alteration of size composition, and truncation of the size composition was thought not to affect future yield because of the inherent resiliency of individuals to exhibit compensatory growth (Handford et al. 1977). However, recent work has shown that alterations in life-history parameters can effect population dynamics (Hutchings 2005).

**Life-history invariants**

Alteration of the frequencies of phenotypes has implications for population dynamics: different phenotypes maximize their fitness in different ways and therefore the dynamics of a population is altered as frequencies of life-histories are altered. An individual has the ability, subject to genetic and developmental constraints (Gould and Lewontin 1979), to allocate resources in an effort to maximize reproductive output. Because resources are finite, an individual necessarily must make trade-offs in allocation decisions; it is not possible to maximize all aspects of growth, reproduction, and survival (Law 1979, Partridge and Harvey 1988). Because of the co-variation in life-history traits as a result of differential allocation of finite resources, there is an inherent correlation of these traits (Charnov 1993, 2002). For example, the value of length-at-maturity, \( L_\alpha \), can be predicted as a function of individual growth rate \( k \), asymptotic length \( L_\infty \), and mean instantaneous mortality rate \( M \) across age-classes (Roff 1992) to maximize reproductive output:

\[
L_\alpha = L_\infty \left( \frac{3k}{3k + M} \right).
\]
Similarly, the predicted age at maturity, $\alpha$, that maximizes the value of $R_0$ in the fitness function was derived by Roff (1984) and Beverton (1992) assuming a constant mortality rate in the population:

$$\alpha = \frac{1}{k} \log \left( \frac{3k}{M} + 1 \right).$$

**The influence of harvest on life-history characters: a review of previous studies**

Inspection of the “invariant relationships” presented above indicates that as the mortality regime or growth characteristics change, correlated parameters will change in a predictable way. Larger individuals typically allocate more energy to somatic growth, mature later in life, and mature at larger sizes (Stearns 1992, Roff 2002). The removal of these fish from a population can result in a spawning stock composed of individuals that reproduce earlier and at smaller sizes (Millner and Whiting 1996, Haugen and Vøllestad 2000, Haugen and Vøllestad 2001, Heino et al. 2002, Grift et al. 2003, Barot et al. 2004). The incorporation of management policies that recognize the ability of fished stocks to respond evolutionarily may be necessary for effective management (Heino 1998, Ashley et al. 2003). Recovery of depleted populations to high abundance has occurred in few cases, and fisheries biologists need to better understand the dynamics of population recovery (Prager and Williams 2003) and the possible effects of fishing to hinder this recovery in an evolutionary context (Hutchings and Reynolds 2004, Walsh et al. 2006). If phenotypic characteristics are largely determined by genetics, then size-selective fishing pressure can, over generations, change the evolutionary trajectory of a population.

Field, laboratory, and simulation modeling work have highlighted the need for conservation of morphological diversity at the population level (Ryman et al. 1995). Size-selective harvest may induce heritable phenotypic effects: some fish populations now are maturing earlier and at
smaller sizes than previously (Millner and Whiting 1996, Haugen and Vøllestad 2000, Haugen and Vøllestad 2001, Heino et al. 2002, Grift et al. 2003, Barot et al. 2004). For commercially harvested species, this shift in life-history traits may affect the productivity of the fishery (Ricker 1981, Conover and Munch 2002) and the ability of the population to rebound to pre-exploitation levels of abundance (Conover et al. 2009).

Researchers have used fishery-dependent and fishery-independent time-series data, controlled laboratory experiments, manipulative field studies, and simulation modeling to describe the dynamics of phenotypic traits in populations (Ricker 1981, Edley and Law 1988, Reznick et al. 1990, Mattingly and Butler 1994, Haugen and Vøllestad 2001, Grift et al. 2003, Conover et al. 2005, Hutchings 2005, Reznick and Ghalambor 2005, Rijnsdorp et al. 2005, Williams and Shertzer 2005). Observational studies of exploited fish stocks, such as the analysis of changes in ages and lengths of maturation over large temporal and spatial scales, are appealing because they support direct inference about how life-history patterns of marine populations have been altered by fishing. A number of alternative hypotheses could explain changes in phenotype: density-dependent processes and alteration of ecosystem conditions (Law 2000, Lorenzen and Enberg 2002, Grift et al. 2003). However, proximal causes of morphological change are difficult to demonstrate unambiguously (McAllister and Peterman 1992, Ryman et al. 1995). Confounding factors may be controlled in manipulative field and laboratory experiments (Conover and Munch 2002). Simulation modeling studies are ideal way to generate testable hypotheses (Pielou 1981). Simulation models can serve as alternative testable hypotheses whose quality in predicting the phenotypic response to selection can be evaluated.
**Review of measurative studies**

Analyses of fishery-dependent data to document historical changes in phenotypic characteristics have been performed on freshwater, anadromous, and marine species. As noted below, these studies document reduction in the age-at-maturity and reduced size-at-age of targeted species, changes that are believed to have resulted from directional selection. The inference that phenotypic change was caused by fishing is robust because comparisons were made from multiple taxa, from long time series and across ecosystems.

Three marine fish stocks, North Sea plaice (*Pleuronectes platessa*), northeast Arctic cod (*Gadus morhua*), and North Sea cod (*G. morhua*) have long time series of length, weight, and fecundity data which allow analyses of historical phenotypic changes (Rijnsdorp 1981, Law and Grey 1989, Grift et al. 2003, Hutchinson et al. 2003, Barot et al. 2004, Olsen et al. 2004, Olsen et al. 2005, Rijnsdorp et al. 2005). Grift et al. (2003) concluded that North Sea plaice have matured at smaller sizes and younger ages because of four decades of fishing. The age at 50% maturity, \( A_{50} \), and the length at 50% maturity, \( L_{50} \), have shifted toward younger ages and smaller sizes. Similar results were reported from an analysis of Atlantic cod from the northwest Atlantic (Olsen et al. 2005). These authors reported that the declining trend in \( A_{50} \) and \( L_{50} \) ceased after a fishing moratorium was imposed and now shows signs of reversal.

Phenotypic evolution also has been reported for freshwater (Handford et al. 1977, Haugen and Vøllestad 2001) and anadromous fishes (Ricker 1981). Haugen and Vøllestad (2001), in an analysis of five allopatric populations of grayling (*Thymallus thymallus*) in central Norway, observed phenotypic changes in adult traits within and among populations: a decrease in the age- and size-at-maturity coincided with alterations in the intensity and size specificity of the gillnet fishery. Handford et al. (1977) reported a decrease in weight- and length-at-age from 1940 to
1975 for whitefish (*Coregonus clupeaformis*) harvested in Lesser Slave Lake, Alberta. The inference that gillnet size-selectivity caused phenotypic change was supported by the observed decline in mean condition and the reduction in the variance of condition, both of which are indicative of directional selection. That is, directional selection increases the relative frequencies of some alleles and combinations of alleles (Dobzhansky 1970), which will change the mean of the phenotypic trait and, by reducing the genetic variation in the population, reduce phenotypic variance.

Ricker (1981) analyzed historical fishery data over large temporal and spatial scales for five species of salmonids from British Columbia to test the hypothesis that fishing was exerting selective pressure on these populations. The case study of pink salmon (*Oncorhynchus gorbuscha*) had the fewest confounding factors and was the most compelling in showing that fishing could cause heritable morphological change: Ricker (1981) reported a decrease in the mean mass of individual pink salmon, from 5.5 to 4.3 lb in odd-year runs and from 4.6 to 3.0 lb in even-year runs in more than half of the stocks. Chum salmon (*O. keta*) did not show a similar reduction in mean size; the detection of any patterns in the mean weight of individuals over time was confounded by regional differences in growth and changes in the dynamics of the fishery. Sockeye salmon (*O. nerka*), like pink salmon, decreased in mean individual weight over the time series, by 0.46 lb in seine and 0.28 in gillnet fisheries. However, inferences about the cause of the decline in mean weight for this stock were complicated by temperature-related geographical differences in growth, characteristics of the fishery, and stochastic fish kills. There was a decrease in size for coho salmon caught in three gears (seine, troll, and gillnet) from 1951 to 1975. Each gear type exerted specific selection pressure: troll-caught coho averaged 1.1 lb and 0.75 lb larger than seined and gillnetted fish, respectively. The decrease in the size of chinook
(O. tshawytscha) salmon over 24 years was dramatic: a mean individual decrease of 5.5 lbs, i.e., a 25 to 50% decrease in mean individual weight that was variable across the geographic range examined. Ricker (1981) concluded that because the observed reduction in mean size occurred across the geographic range examined and over decades, genetic effects may be responsible for the shifts in phenotype.

**Review of manipulative lab and field experiments**

Manipulative laboratory and field experiments can be powerful because they can limit confounding explanatory factors that may be present in purely observational studies. Reznick and Ghalambor (2005) synthesized the results of multiple experiments and documented changes in the life history of guppies (Poecilia reticulata) in response to differential natural mortality caused by predation. Guppies in Trinidadian mountain streams are a convenient experimental system for testing the effects of predation because natural barriers in streams preclude movement and allow predator densities to be manipulated. Individuals from high-predation regimes matured earlier and produced more offspring of lower mass. Conversely, the offspring from low-predation areas reached maturity later, and produced fewer, larger offspring. The authors hypothesized that the rate of evolution may be greater (in terms of generation time) for harvested fish populations because of the greater intensity of fishing pressure relative to natural mortality.

Shifts in life-history have occurred in laboratory animals that were subjected to size-specific culling. Conover and Munch (2002) culled populations of Atlantic silversides (Menidia menidia) such that the largest 90% of individuals were removed from two replicates, 90% of the smallest from two replicates, and a random 90% from two control replicates. Over four generations, the offspring of each cohort provided subjects for culling in subsequent generations.
In the large-harvest replicates, the mass of harvest and the mean weight of culled fish declined over four generations, while egg sizes and rates of larval development decreased significantly. In a similar experiment, Edley and Law (1988) evaluated replicated treatments of the cladoceran *Daphnia magna* under two size-specific culling regimes, in which large or small individuals were removed from each generation. Forty to fifty percent of individuals were removed over the 48-day experiment. Culling small individuals resulted in successive generations growing relatively quickly for the first six size stages (size classes based on mesh size of nets used for culling). When large individuals were removed, offspring took twice as long to reach vulnerability to harvest in a similar mesh size as individuals in the small-cull treatment.

Given the results from studies and the theoretical aspects of quantitative genetics and life-history processes, it is reasonable to hypothesize that fishing mortality can act as a selective agent if the phenotypic characteristics that are targeted have a heritable basis. In addition to FIE, the existence and relevance to management of evolutionary processes has been recognized in a number of disparate disciplines, including medicine (Nesse and Stearns 2008), agronomy (Palumbi 2001), and natural resource management (Conover and Munch 2002, Reznick and Ghalambor 2005). That human interactions cause the systematic removal of individuals that exhibit similar phenotypes changes their relative fitness and alters population dynamics has been described. Recent work, however, has documented that these trends in ‘evolutionary downsizing’ are reversible with the relaxation of fishing (Conover et al. 2009), at least in some cases. The challenge for fishery managers is to reconcile management actions that focus upon sustainability with the quantitative genetics processes that occur as the result of FIE.
**Objectives of this dissertation**

I have four major objectives of this dissertation. The first is to determine the suitability of Japanese medaka for selection experiments and to also describe its husbandry and life-history characteristics. I then describe the results of a selection experiment using Japanese medaka; specifically I report how morphology and life-history characteristics change over multiple generations of selection. I use the patterns of life-history and morphology observed in the selection experiment to validate individual-based simulation model predictions using Japanese medaka life-history characteristics. Finally, I use the individual-based simulation modeling, incorporating life-history characteristics of Atlantic cod *Gadus morhua*, to determine how biological and fishery characteristics change in a large, age-structured population exposed to size-selective fishing over multiple generations.
LITERATURE CITED:


Chapter 1.
Life-history Characteristics of Japanese medaka *Oryzias latipes*

**ABSTRACT:**

Japanese Medaka *Oryzias latipes*, is a widely used organism in biological investigations because of its high fecundity, small adult size, and ease of husbandry. However, many aspects of its life history have not been fully described. I modeled the length-at-age relationship with three commonly used growth models; a two-parameter von Bertalanffy growth function (VBGF), a three-parameter VBGF and the Richards function. I found that the Richards function provided the best description of mean length-at-age: $L_\infty = 39.2$ mm TL, $k = 0.028$ dph$^{-1}$, $\beta = -0.39$, and $n = 8.46$. Three-parameter VBGF estimates were used to predict longevity of 347 to 485 days. The weight-at-length relationship was described using a power curve and resulted in mean parameter estimates, $a = 2.16 \times 10^{-5}$ and $b = 2.79$. The mean proportion of viable eggs that hatched to larvae was 73% (95% confidence interval 53 to 93%). I observed that 50% of larvae emerge from eggs at 3.3 days and 100% of larvae emerge at 9 days following collection. Daily egg production increased to its maximum number (range 8 to 48) of eggs at 85 to 91 dph (days post-hatch). Total egg production by individual females ranged from 38 to 141 eggs. We found a significant negative linear relationship ($P < 0.001$, $R^2 = 0.28$) between the number of eggs collected from an individual during a single egg deposition event ($n = 91$) and mean egg volume (mm$^3$). However, there were variations in the sizes of individual eggs (CV $\times$ 100 = 6.5). My work provides previously unreported life-history information that can be used to develop experiments in the laboratory and field and increase understanding of this species.
INTRODUCTION:

A great diversity of organisms are used for laboratory manipulation, and fishes have a long and rich history of use in biological experimentation (Fabacher and Little, 2000). The use of fishes as model organisms for hypothesis testing is widespread and includes their use in investigations for ecology, development, genetics, toxicology, pharmacology and other applications. The selection of a particular fish species for a study involves balancing the husbandry needs of the species and the specific research goals of the study (DeTolla et al., 1995). A knowledge of the natural history of a candidate species is desirable (Mayer, 2004).

Japanese Medaka *Oryzias latipes* has been widely used in experimental biological investigations (Wolgemuth et al., 1997; Wittbrodt et al., 2002; Kinoshita et al., 2009). Japanese Medaka is a freshwater member of the family Adrianichthyidae, the rice fishes, and is indigenous to Japan, Korea, Vietnam, and China, where it is found in marshes, ponds, and rice paddies (Takehana et al., 2003; Takehana et al., 2004). In some areas of their native range, Japanese Medaka are considered at risk due to loss of habitat (Takehana et al., 2003). However, cultured stocks are available from academic institutions and commercial suppliers of aquatic research organisms.

Fishes are selected for experimental work, in part, because of their ease of husbandry and their high population growth rates (Overstreet et al., 2000). Japanese Medaka has been reported to tolerate a wide range of temperatures (Yamamoto, 1975; Shima and Mitani, 2004), enabling breeding and husbandry in outdoor enclosures (Kinoshita et al., 2009) as well as in aquaria. Japanese medaka exhibit prolific and oviparous egg production that is initiated at 25 to 30 mm SL and controlled by the intensity and duration of the photoperiod (Egami, 1954; Shima and Mitani, 2004). Females produce eggs that are carried on the outer ventral surface, where they
can be collected directly from the fish (Kirchen and West, 1976; Kinoshita et al., 2009). The reported longevity in the wild is generally one year and can be as great as five years in captivity (Shima and Mitani, 2004). Japanese medaka reach a reported maximum size of 32 mm SL in the wild (Nakabo, 2002).

With the exception of some descriptive (Yamamoto, 1975; Kirchen and West, 1976; Dhillon and Fox, 2004) and experimental work on early life history (Teather et al., 2000), little information has been reported on aspects of life history of Japanese medaka. Here, I report biological and husbandry characteristics of a laboratory-maintained population of Japanese medaka descended from crossbreeding and inbreeding of nine commercially available and wild populations. I determine patterns of somatic growth (length-at-age and weight-at-length relationships), describe the developmental competency of collected eggs and their sources of mortality, egg characteristics (the frequency of egg production, the relationship of egg volume to clutch size), and the effects of egg size on rates of larval development. These results contribute to an understanding of the ecology of the Japanese medaka and provide life-history information for those interested in using this organism for experimental investigations.

MATERIALS AND METHODS:

Broodstocks, representing nine of populations, of Japanese medaka used for this study were obtained from the National Institute for Basic Biology, Niigata University, Japan and from a commercially available source in the United States (Table 1). These individuals were reared to reproductive age and interbred for two generations to maximize genetic variation for ancillary experiments. The crossbred population was maintained at the Freshwater Mollusk Conservation Center at the Virginia Polytechnic and State University, Blacksburg, Virginia, USA.
Adult Japanese medaka were maintained in a multi-tank recirculating aquaculture system consisting of twelve 75.7-L tanks and a central 1000-L sump. Water was circulated using a 0.75-hp centrifugal pump that maintained water flow to each tank at a rate of 13.1 L min\(^{-1}\). Water source was a mix from a well and from a treated municipal supply and was maintained at 26.5°C (± 2.2°C SE) using submersible aquarium heaters. Water quality was maintained with biological filtration (Aquatic Ecosystems® BioBarrels), mechanical filtration (fluidized bead filter), and a 40-WUV filter, as well as frequent water changes. Individual lights in each tank (18-W fluorescent lamps) were used to maintain 14:10 daily light:dark cycle that was used throughout the study. Each tank was wrapped with black plastic to seal it from external light sources. Tanks were cleaned once every 1-2 days to remove feces and uneaten food.

Larvae were hatched from eggs and collected to populate each tank over a maximum period of seven days. The age of individual larvae in each tank was estimated as the median number of days post-hatch (dph) from collected eggs. Tanks contained individuals whose ages were known based on their similar hatching dates. All individuals, after hatching, were housed in the multi-tank recirculating system. There were differences in the care of different age-classes with respect to water flow, diet, and density. Tanks that held fish younger than 60 dph had outflows fitted with 2.54-cm reticulated foam to minimize mortality of juveniles. At ages of approximately 60 dph, the foam filter housing was removed and replaced with an outlet strainer. All fish in the experiment were fed two to three times daily. Fish less than 30 dph were fed with Zeigler® larval diet (≥ 40% protein, particulate size < 100 μm). Individuals 30 dph or older were fed with ground Aquatic Ecosystems® tropical flake food (≥ 40% protein) and live brine shrimp every seven to ten days. The density of individuals (≤ 75 dph) in each tank ranged from 133 to 335, but upon reaching age 75 dph the number of individuals in each tank was equalized to 60.
Total length (TL, mm) and weight (g) of fish in the experiment were recorded and used to determine ontogenetic patterns of somatic growth. The total length of fish \( \leq 60 \) dph was determined by digital image analysis. Images of known-age fish were obtained by placing fish in a shallow tank over a grid of known scale and taking a picture with a digital camera (5.0 megapixel). The image was analyzed using the digital image analysis program, Image Pro-plus (version 6.1, Media Cybernetics, Inc., Bethesda, MD, USA), and the total length of each individual was determined by converting the number of pixels to millimeters using the scale of the grid system as a reference. Japanese medaka older than 60 dph were measured with calipers. Preliminary work indicated that there was no significant difference in the measurements derived using the two alternative measurement methods. We measured a subset of adults (\( n = 30 \)) for both total length (tip of snout to end of caudal fin) and standard length (tip of the snout to the distal end of the caudal peduncle) and evaluated the relationship of the two measures using linear regression. I tested three commonly used growth models to describe the length-at-age relationship. The first was the three-parameter von Bertalanffy growth function (VBGF):

\[
L_t = L_\infty (1 - e^{-k(t-t_0)})
\]

where \( L_\infty \) is the maximum average expected TL mm of all individuals used in the length-at-age analysis, \( k \) is the von Bertalanffy growth rate constant (dph \(^{-1}\)), and \( t_0 \) is the theoretical age at length zero mm TL. Variables in all of the growth models presented are \( L_t \), the length (TL mm) of each fish at age \( t \) (dph). The second growth model used to describe the length-at-age relationship was the two-parameter VBGF:

\[
L_t = L_\infty (1 - e^{-k_t})
\]
This model is identical to the three-parameter model, but does not include the parameter $t_0$, which is assumed to be zero. The third model used to analyze the length-at-age relationship is the four-parameter Richards function (Ebert, 1981):

$$L_i = L_\infty (1 - \beta e^{-kt})^{-c}.$$ 

This model is identical to the VBGF when the shape parameter $c$ is equal to $-1$, with the exception of the inclusion of the parameter $\beta$. The parameter $L_\infty$ is the maximum average expected TL of all individuals used in the length-at-age analysis and $k$ is the growth rate constant (dph$^{-1}$). Nonlinear curve-fitting was used to estimate each parameter and its 95% confidence interval. Each of the length-at-age models was analyzed for goodness-of-fit using Akaike’s information criteria (AIC) (Burnham and Anderson, 2002) which is defined as:

$$AIC = 2K + n \ln(\hat{\delta}^2).$$

Where K is the number of model parameters estimated and n is the number of data points. The estimated variance $\left(\hat{\delta}^2\right)$ for each model is equivalent to RSS$/n$. RSS is the residual sum of squares of the non-linear model. The value $\Delta AIC_{model}$ is a criterion of comparison among models and is determined as the difference between the AIC of the model under consideration and that of the model that is considered the best fit, the one with the lowest of AIC value.

Longevity, $\omega$, was calculated as the age (dph) taken to reach 95% and 99% of predicted $L_\infty$ estimated from the three-parameter VBGF model (Fabens, 1965; Ricker, 1979), and these estimates are estimated:

$$\omega_{\text{Ricker 1979}} = \frac{5 \log_e 2}{k}$$

and
$\omega_{\text{Fabens}1965} = \frac{7 \log_e 2}{k}.$

We used a two-parameter power curve to describe weight-at-length:

$$W = aL^b.$$  

$W$ is an individual’s wet weight (g) and $L$ is an individual’s length (TL mm). Individual weight was determined with a digital balance. Only the weights of fish 60 dph or older were taken to avoid mortality of young fish.

I determined a variety of reproductive characteristics, including the total number of larvae produced from batches of eggs, the rate of larval production from eggs, and the magnitude of egg production during the breeding season. Eggs were obtained by removing them directly from females; a micro-spatula was used to gently scrape the clumped egg mass that was held external to the body. The eggs were separated from one another and from debris (uneaten food and feces). Only those eggs that were fertilized and potentially viable were used for analysis. Groups ($n = 68$ to $96$) of eggs, randomly collected with respect to individual and maternal condition (age, length, weight), were allocated to one of nine aerated incubation jars. Incubation jars were 1-L glass mason jars immersed in a temperature-controlled water bath (range 25 to 27°C). A rigid acrylic tube (outer diameter 4.76 mm) was inserted into the lid of each jar and was attached to an air pump. The flow of air was regulated using a central manifold and set to the minimum amount of air pressure necessary to keep the developing eggs in suspension in each jar. Three drops of 0.1% aqueous methylene blue ($\text{C}_17\text{H}_{18}\text{CIN}_3\text{S}$) were added to each jar to inhibit fungal growth and pathogen development. The water in each incubation jar was composed of an equal mix of well water and treated municipal supply and was changed daily.

The number of larvae collected and sources of egg mortality were assessed. Eggs that were unfertilized or did not exhibit larval development were considered dead and were removed.
In this case the yolk of the egg turned opaque after one or more days and cell division was limited or absent. Additionally, eggs that showed signs of pathogenic infestation (bacteria and/or fungal growth) were enumerated and also removed. We determined the number of eggs that resulted in hatched larvae for each of the nine replicates. The rate of larval production was described using a two-parameter logistic function:

\[
\%Larvae = \frac{1}{1 + e^{-\lambda(day - \phi)}} .
\]

The parameter \(\lambda\) is the steepness of the logistic curve and \(\phi\) describes the number of days corresponding to 50% production of the total number of larvae produced (the inflection point of the logistic function).

To determine the magnitude of egg production by Japanese medaka, I used an experimental system similar in design to that proposed by Cattin and Crosier (2004). The apparatus consisted of PVC tubes (15.2 cm outer diameter and 17.8 cm height), such that each tube enclosed 5.7 L. Tubes were open at the top and sealed on the bottom with 0.5 mm mesh. Tubes were suspended vertically in a tank (170 L) that was incorporated into the recirculating system described above. Randomly selected immature females \((n = 9,\) ranging from 29.0 to 34.5 mm TL) and mature males \((n = 18)\) were allocated to each of nine tubes (two males and one female per tube). The feeding regimen was identical to that described above and water was distributed to each isolated tube at a flow rate of 1.2 L min\(^{-1}\). Egg production was monitored every one to two days from its onset to termination in each replicate. Eggs were collected directly from females or removed from the enclosure during daily cleaning. The temporal pattern of daily egg production was modeled using a three-parameter Gaussian density function (Rogers-Bennett et al., 2007):
Where the estimated daily egg production, \( E \), is a function of the model parameters \( A \) (the maximum egg production), \( \mu \) (the age of maximum egg production, dph), and \( \sigma \) (the standard deviation of the age of maximum egg production).

The magnitude of daily maternal investment (mm\(^3\) egg volume) was determined for each female by collecting eggs directly from females. Eggs were measured using digital image analysis and, because Japanese medaka eggs are nearly spherical, I measured the radius of each egg to estimate egg volume. Linear regression was used to describe the relationship of mean egg volume to the number of eggs collected in each clutch.

To determine the relationship of mean egg volume to the average TL of larvae, I collected egg masses from mature females of known age (age range = 74 to 132 dph) and size (length and weight). Egg volumes were determined and eggs from each clutch were incubated, as a group, in the incubation system. Upon detection of hatching, the swimming larvae from each clutch were measured (TL mm) using digital image analysis.

**RESULTS:**

The relationship of SL to TL was determined by linear regression; \( SL = 0.83 \times TL - 0.16 \) \((P < 0.001, R^2 = 0.92, \text{Table 2})\). Mean growth model parameter estimates were determined from 2327 measurements taken from 990 individuals (Figure 1a, Table 2). I found that the Richards function provided the best fit to the length and age data (AIC = 6469.4) relative to the two- and three-parameter VBGF models (\( \Delta \text{AIC}_{\text{VBGF 2-parameter}} = 261.1 \) and \( \Delta \text{AIC}_{\text{VBGF 3-parameter}} = 216.4 \)). For each formulation of the VBGF examined the mean value of \( L_\alpha \) was greater than the largest individuals the oldest ages examined (285 dph). Estimated longevity based on the three-
The mean proportion of eggs that hatched in each replicate was 73%, but was highly variable across replicates (95% confidence interval 53 to 93%). The mean proportion of eggs that died was 18% (95% confidence interval 12 to 28%), and the mean proportion of eggs infested by bacteria or fungi was 6% (95% confidence interval 7 to 17%). Larvae hatched from eggs as soon as 1 day following egg collection. On average, all larvae hatched after 7 days of incubation. Although I regarded larvae hatched when they were completely free of their egg capsules, there were individual differences in the corresponding developmental stages of such larvae. These ranged from individuals that were non-mobile and retained a visible yolk sac to those that were free-swimming and exhibited a greatly reduced yolk sac.

The logistic regression for hatching rate of larvae in the incubation system exhibited significant differences certain some replicates in the steepness and number of days associated with 50% of total larvae production (Fig. 2). Seven of the nine replicates were statistically similar ($\alpha = 0.05$) in both parameters; pooled means were $\lambda = 1.4$ and $\varphi = 3.3$ days (Fig. 2, Table 2). Two replicates differed from the pooled estimates of the number of days to reach 50% egg production (both were greater, mean number of days: 4.1 and 6.3). Each of these two replicates also differed in the rates of hatching as determined by the steepness parameter, mean value = 0.84 and 0.78, indicating that development of larvae was slower in each of these replicates relative to the pooled estimates.
Total individual egg production of the nine females during the course of the study ranged from 38 to 141. Egg production was initiated at 76 to 77 dph for most replicates (Fig. 3) and increased to a maximum level of production of 8 to 48 eggs day$^{-1}$ at approximately 91.2 dph and then declined. The magnitude of daily egg production for each of the replicates was pooled for those replicates whose non-linear model parameters were statistically similar ($\alpha = 0.05$, Table 2). The mean values of the pooled parameters were $A = 23.8$ eggs, $\mu = 91.2$ dph, and $\sigma = 7.7$ dph. One replicate (28.5 mm TL, 0.311 g) differed significantly in two aspects of daily egg production; its predicted maximum value of egg production occurred at an earlier age ($\mu = 85.3$ dph) and this occurred over a narrower range of ages ($\sigma = 2.9$ dph; Fig. 3).

There was a significant negative linear relationship ($P < 0.001$, $R^2 = 0.28$) between the number of eggs collected from an individual during a single egg deposition event (1193 eggs, measured from 92 individuals) and the mean egg volume (Fig. 4a). However, there were variations in the sizes of individual eggs within a clutch ($CV \times 100 = 6.5$). The range in lengths of larvae upon hatching was 3.6 to 5.8 mm TL. Mean length (TL mm) at hatching and mean egg volume (mm) were positively though not significantly correlated ($P = 0.18$, $R^2 = 0.24$; Fig. 4b).

**DISCUSSION:**

The results of this study contribute to the understanding of ontogenetic development, egg production, and larval dynamics of captive-reared Japanese medaka. To my knowledge, quantitative analyses of many life-history characteristics of this species have not been previously reported. I describe the sources and the magnitude of egg mortality and found that the rate of development of larvae from eggs may be more rapid than previously reported (Teather et al., 2000). Although the magnitude of daily egg production was variable, the age of maximum
production was conserved among most replicates. Finally, I observed a significant negative relationship between daily reproductive output and maternal investment, measured by egg volume.

The von Bertalanffy growth function is widely used to describe the non-linear relationship of length-at-age of fishes (Cailliet et al., 2006); however, other candidate models are often used to describe ontogenetic growth. In this case, I found that the Richards model best described medaka length-at-age. The estimates provided by each of the VBGF models were precise, but overestimated the maximum mean TL. Morphological variability of populations in the laboratory might be expected to be lower than that for the same trait measured from wild populations because of constancy of environmental conditions. However, the genetic nature of the population we examined is different from that found in the wild; the study population was comprised of crossbred offspring from parents sourced from multiple locations in mainland Asia and Japan as well as from stocks commercially available in the United States (Table 1). Although Japanese medaka occur in similar habitats in Japan, Korea, and southeast China, these populations are allopatric, and exhibit molecular divergence (Takehana et al., 2003; Takehana et al., 2004). The population that I characterized is the F3 generation from interbreeding of individuals from these disparate populations, and the variation in somatic growth that we observe may be affected, to some extent, by outbreeding processes. The fit of the VBGF to the observed data was poor at the maximum age (285 dph). It is desirable that the length-at-age data be collected over the entire range of ontogeny (Beamish and McFarlane, 1983; Campana, 2001) for accurate determination of somatic growth relationships. Our mean estimate of asymptotic length (47.3 mm TL, 38.9 cm SL [95% CI 33.8 to 44.0 mm SL]) was significantly greater than the maximum SL estimate (32 mm) previously reported (Shima and Mitani, 2004). The longevity
estimate, \( \omega \), that I report is based on the calculated mean growth rate, \( k \text{ dph}^{-1} \) and is similar to that reported for Japanese medaka held in mesocosm conditions for one year (Shima and Mitani, 2004). The power curve fit to weight and length measurements indicated that there is variability among individuals at lengths that exceed 30 mm TL. The observed variance at these larger lengths may be a result of female condition after a reproductive event. Spawning result in the immediate loss of mass and hence condition.

Information about the rate of larval production and the expected developmental competency of eggs is useful for planning and executing experiments using captive animals. We found that the lower 95% CI estimates of the proportion of larvae produced from eggs is 53%. This value represents a conservative estimate of the proportion of larvae that an experimenter can expect for a given group of eggs. The rate of development from egg to larvae is controlled by a number of experimental conditions, and differences in the rates that we report to those previously reported may be a result of such differences. Most notably, temperature controls the rate of larval development, and Kirchen and West (1976) recommended an incubation temperature of 25°C ± 0.5°C. In their descriptive scheme of egg developmental stages, these authors reported that Japanese medaka larvae emerge from the egg at ~11 days after egg collection. Teather et al. (2000) reported that 42% of larvae hatched between 9 to 11 days after egg collection. In contrast, we found that Japanese medaka hatched earlier; 100% of larvae had emerged from eggs in each of our replicates within seven days (Fig. 2). One feature of larval emergence was the variety of developmental stages that larvae exhibited upon hatching. Although I observed the emergence of larvae from eggs in many stages of development, no replicates in the experiment produced larvae after 9 days of incubation. Teather et al. (2000) found that hatching continued to day 35. It is probable that the differences in emergence times may be attributed to environmental conditions.
including water quality, temperature, or the use of aeration in our incubation system. The use of aeration serves to reduce pathogen development and may promote early emergence of larvae, though these hypotheses needs to be tested. Two replicates exhibited significantly longer mean time to hatching (Fig. 2), but the timing of hatching of these replicates was still less than that reported by Teather et al. (2000). Because the eggs that comprise each of the replicates were drawn from the same pool, the values of $\phi$ that we report describe the range of possible development times.

In addition to information about hatching rates, the expected magnitude of egg production is of considerable utility to experimenters. Egami (1959) reported that lifetime production of Japanese medaka is typically 1000 to 2000 eggs (and up to 3000 eggs) and Kinoshita et al. (2009) reported that 10 to 20 adults can produce 20 to 50 eggs per week. I found that the magnitude of egg production during the study period is 38 to 126 eggs per female. I examined breeding only during the first breeding period, and it is possible that egg production may increase for even older females. A variety of additional abiotic conditions may account for differences in individual egg production, including photoperiod (Yamamoto, 1975). The fish in my system were exposed to 14 hours of daylight, and this may have artificially limited egg production. In captive rearing of Zebrafish *Danio rerio*, the rate and magnitude of egg production can be manipulated by altering the duration of light during ontogeny (Westerfield, 2005). Westerfield (2005) reported that egg production of Zebrafish can be manipulated, and that a 14:10 hour light:dark cycle is optimal for the continuous production of a relatively small number of eggs. We found that egg production is initiated at 76 dph, is terminated at 115 dph, and is maximized at 85 to 92 dph. In ancillary experiments, I found that egg production commenced as early as 58 dph and terminated at 147 dph. The individual that exhibited elevated
egg production (Fig. 3), at an earlier age, was similar in length and weight to the other individuals monitored. The statistically different relationship in the Gaussian parameters that I observed for this individual may be a result of model misspecification. The greatest reproductive output occurred at an age $\leq 95$ dph. A non-symmetric, non-linear curve may better accommodate the observed patterns in age-specific egg production. However, model fit to data was not improved when I used a three-parameter, log-normal curve.

Life-history theory predicts tradeoffs in the ability of an organism to invest energy during development (Reznick, 1983). I report one such tradeoff in the statistically significant negative correlation between clutch size and mean egg size (Fig. 4A). Although the magnitude of reproductive output is mediated by physiological attributes (length, weight, and age; Teather et al. 2000), there may be physiological or fitness trade-offs to produce more, small eggs or fewer, large eggs. Although the relationship is linear and statistically significant, there was large variability ($R^2 = 0.28$) that may be result of alternative strategies in the timing of egg production.

I detected a weak positive correlation between mean egg volume and the total length of larvae. The experimental design I used to determine this relationship lacked statistical power and was confounded by both measurement error and the design of the experiment. Japanese medaka larvae emerge from the egg and generally develop rapidly; an individual absorbs its yolk sack, becomes motile, and initiates exogenous feeding within hours after emergence (Kirchen and West, 1976). Our measurements of hatched Japanese medaka larvae did not account for the variation in post-hatch development that occurred between the time of hatching and my detection, contributing to the variance of lengths of larvae within a clutch. Additionally, limitations in my experimental system necessitated that eggs be incubated as a group and larval characteristics such as length-at-hatching could not be assigned to a single egg.
The information presented here contributes to understanding of life-history dynamics of Japanese medaka. In addition to information relevant for conservation and management of this species, which is under threat of extirpation in its native range (Takehana et al., 2003; Takehana et al., 2004), the information about the demographic patterns of Japanese medaka is relevant to theoretical ecology. Increasing understanding of the diversity of life-history patterns and ontogenetic tradeoffs allows experimenters to make inferences about evolutionary constraints and their role in the ecology of this and other taxa. Finally, many genetic and ecological investigations would benefit from using additional and different research organisms. The life history of Japanese medaka makes it suitable for a range of studies, and the information presented here should prove helpful in use of this organism for research.
LITERATURE CITED:


Table 1.1. Source, population names, and source locations of Japanese medaka *Oryzias latipes* populations used as broodstock in this study. These individuals were interbred for two generations (F1 and F2) and life-history characteristics of individuals from the F3 generation were analyzed as described in the text. The population names reflect the geographically derived genetic subdivisions described by Takehana et al. (2003, 2004), map numbers can be referenced in those studies.

<table>
<thead>
<tr>
<th>Source</th>
<th>Population</th>
<th>Location of broodstock collection (and map reference)</th>
<th>Number of adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niigata University, Japan</td>
<td>Northern</td>
<td>Hamochi (82)</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Honjo (17)</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Southern</td>
<td>Odawara (78)</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kesennuma (9,10)</td>
<td>10</td>
</tr>
<tr>
<td>East Korea</td>
<td>Gwangeui</td>
<td>Gwangeui (50)</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Paltan</td>
<td>Paltan (5)</td>
<td>3</td>
</tr>
<tr>
<td>China-West Korea</td>
<td>Cangwon</td>
<td>Cangwon (59)</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Suncheon</td>
<td>Suncheon (48)</td>
<td>6</td>
</tr>
<tr>
<td>Carolina Biological Supply</td>
<td>–</td>
<td>–</td>
<td>120</td>
</tr>
</tbody>
</table>
Table 1.2. Quantitative analyses of life-history and morphological traits of Japanese medaka *Oryzias latipes*.

dph is days post-hatch and all lengths of fish are in mm total length (TL).

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Model</th>
<th>Model name</th>
<th>Estimated parameter values (mean ± 95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length (mm) vs. Total Length (mm)</td>
<td>$SL = β_0 + TL \times β_1$</td>
<td>Linear</td>
<td>$β_0 = -0.16\text{ mm } (-3.2\text{ to } 2.8)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$β_1 = 0.83\text{ (0.73\text{ to } 0.92)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$L_∞ = 49.5\text{ mm TL } (47.3\text{ to } 51.6)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$β_0 = -0.39\text{ (−0.42\text{ to } −0.35)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$c = 8.46\text{ (7.98\text{ to } 8.93)}$</td>
</tr>
<tr>
<td>Length-at-age</td>
<td>$L_t = L_∞(1 - e^{-k(t-t_0)})$</td>
<td>3-parameter VBGF</td>
<td>$k = 0.010\text{ dph}^{-1}\text{ (0.009\text{ to } 0.011)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$t_0 = 3.3\text{ dph (2.0\text{ to } 4.6)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2-parameter VBGF</td>
<td>$L_∞ = 50.7\text{ mm TL } (48.6\text{ to } 53.7\text{ mm TL})$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$k = 0.00947\text{ dph}^{-1}\text{ (0.0087\text{ to } 0.010\text{ dph}^{-1})}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$L_∞ = 39.2\text{ mm TL } (38.3\text{ to } 40.1)$</td>
</tr>
<tr>
<td>Length-at-age</td>
<td>$L_t = L_∞(1 - e^{-kt})$</td>
<td>3-parameter VBGF</td>
<td>$k = 0.028\text{ dph}^{-1}\text{ (0.027\text{ to } 0.030)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$β = -0.39\text{ (−0.42\text{ to } −0.35)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$c = 8.46\text{ (7.98\text{ to } 8.93)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$L_∞ = 50.7\text{ mm TL } (48.6\text{ to } 53.7\text{ mm TL})$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$k = 0.00947\text{ dph}^{-1}\text{ (0.0087\text{ to } 0.010\text{ dph}^{-1})}$</td>
</tr>
<tr>
<td>Weight-at-length</td>
<td>$W = aL^b$</td>
<td>Power curve</td>
<td>$a = 2.16 \times 10^{-5}\text{ (1.77 \times 10^{-5}\text{ to } 2.55 \times 10^{-5})}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$b = 2.79\text{ (2.73\text{ to } 2.84)}$</td>
</tr>
<tr>
<td>Mean longevity</td>
<td>$\frac{5\log_c 2}{k} \text{ and } \frac{7\log_c 2}{k}$</td>
<td>95% and 99% of predicted $L_∞$</td>
<td>$387\text{ to } 485\text{ dph}$</td>
</tr>
<tr>
<td>Rate of larval production*</td>
<td>$%\text{Larvae} = \frac{1}{1 + e^{-λ(\text{day−φ})}}$</td>
<td>2-parameter logistic function</td>
<td>$λ = 1.4\text{ (1.1\text{ to } 1.6)}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$φ = 3.3\text{ days (3.1\text{ to } 3.4)}$</td>
</tr>
<tr>
<td>Analysis</td>
<td>Model</td>
<td>Model name</td>
<td>Estimated parameter values (mean ± 95% CI)</td>
</tr>
<tr>
<td>----------------------------------------------</td>
<td>-----------------</td>
<td>---------------------------------</td>
<td>--------------------------------------------</td>
</tr>
<tr>
<td>Temporal pattern of daily egg production*</td>
<td>( E = Ae^{-0.5(x-\mu)^2/\sigma^2} )</td>
<td>Gaussian density function</td>
<td>( A = 23.8 ) eggs (18.8 to 27.6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>( \mu = 91.2 ) dph (89.6 to 92.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>( \sigma = 7.7 ) dph (6.2 to 9.1)</td>
</tr>
</tbody>
</table>

*Pooled estimates of replicates with similar model parameters are presented. Statistically different parameters of some replicates observed in each analysis are presented in the text.
Figure 1.1. Mean length-at-age (A) and weight-at-length (B) for Japanese medaka. Mean length-at-age was estimated using a three-parameter von Bertalanffy growth function (black dotted line), a two-parameter von Bertalanffy growth function (gray dashed line), and the Richards function (gray dashed line). The weight-at-length relationship was described using a power function ($a = 2.16 \times 10^{-5}$ and $b = 2.79$, $n = 1532$).
Figure 1.2. Daily larval production of Japanese medaka from collected eggs. The mean rate of egg production was described using a two-parameter logistic function. Replicates with similar model parameters \( (n = 7) \) were combined (the mean and the predicted 95% confidence intervals are displayed with gray lines). Mean parameter estimates for two replicates differed significantly in model parameters and were plotted separately with solid and dashed black lines.
Figure 1.3. Daily production of eggs collected from female Japanese medaka (age range 76 to 115 days post-hatch, dph). Data were modeled with a three-parameter Gaussian density function (gray solid lines are the mean and predicted 95% confidence interval from pooled replicates, $n = 8$). A single replicate differed significantly for two model parameters, and results are represented by a dashed black line.
Figure 1.4. The relationship of mean egg volume to clutch size (A) and the relationship of the mean size of larvae and mean egg volume (B) for Japanese medaka. Error bars for A and B are mean ± SE.
Chapter 2.

Inter-generational effects of length-selective culling on morphological characteristics of Japanese medaka (*Oryzias latipes*)

**ABSTRACT:**

Anthropogenic impacts on natural populations include phenotype-based selection, such as length-selective fishing on harvested fish populations. Size-selective fishing has been shown to alter the evolutionary trajectories of morphology and life-history of populations. In this study, I describe the multigenerational effects of length-selective removal on weight- and length-at-age (and their associated heritabilities), patterns of change in somatic growth relationships (weight-at-age and linear early growth), and patterns of egg production on the laboratory model organism, Japanese medaka *Oryzias latipes*. Twelve lineages divided equally among three treatment levels (removal of 80%, 40% of the largest individuals and a control) from populations of medaka were observed for four generations (*n* = 300 individuals). The treatment effects did not alter the morphological point estimates of pre-cull 75-dph (days post hatch) length and 75-dph weight. The estimated mean heritability of 75-dph length was not significant (0.44, 95% CI = −0.15 to 1.73, $R^2 = 0.41$), however, the mean heritability estimate of 75-dph weight was significant (0.43, 95% CI = 0.24 to 0.62, $R^2 = 0.66$). I observed changes in allometric growth relationships, indicating that the fish were becoming increasingly elongated and less deep-bodied. Although no significant decreases in either the number of eggs produced per reproductive event or egg size occurred in concert with morphological change, I did observe that the mean age that reproduction occurred decreased among generations for the 80% removal treatment. The alteration of fitness-related processes that co-vary with length and weight may
occur even if there are no observable changes in mean somatic growth characteristics, posing
implications for fishery management.

INTRODUCTION:

Studies from natural and human-impacted populations have documented many examples of
directionally selective processes that constrain and direct phenotypic expression over
contemporary time scales; examples include Darwin’s finches and bighorn sheep (Grant and
Grant 1995, Coltman et al. 2005). Directional selection occurs when a subset of individuals in a
population, because of their shared similarity in one or more phenotypic traits, is exposed to a
greater rate of mortality than individuals in the remainder of the population (Falconer and
Mackay 1996). In natural populations, the presence of predators or adverse environmental
conditions may act as agents of directional selection (Grant and Grant 1993, Mattingly and
Butler 1994). Human impacts such as pathogen control in agriculture and medicine, can also
result in changes in the composition of the phenotypes in a population (Williams and Nesse

The immediate response of a population to directional selection is ecological: the dynamics
of the population are determined by the phenotypes that remain in the population. This aspect of
selective removal is of considerable interest to fishery biologists concerned with predicting
population resilience and the effects of harvest – the demographic qualities of the population are
determined by the population’s phenotypic composition. In the case of fishery harvest, an
emerging hypothesis about the previously unaccounted-for effects of removal, termed fishery-
induced evolution, is becoming prevalent (Kuparinen and Merilä 2007, Hutchings and Fraser
2008). The FIE hypothesis that harvest can alter the frequencies of phenotypes is based on
observed changes in the phenotypic characteristics of individuals of harvested populations (Heino et al. 2002, Olsen et al. 2004, Olsen et al. 2005) and the predictive effects of quantitative genetics processes (Ricker 1981). The FIE hypothesis has been used to explain the observed historical changes in morphology and life-history characteristics, such as length-at-age and age-at-maturity for Atlantic cod (Gadus morhua) and North Sea plaice (Platessa platessa) (Hutchings 2005, Rijnsdorp et al. 2005). Other examples of contemporary evolutionary processes have been observed in brook charr (Salvelinus fontinalis) and Pacific salmon (Oncorhynchus spp.) populations (Ricker 1981, Hard et al. 2008, Theriault et al. 2008).

The principles of quantitative genetics require three conditions for evolution of a phenotypic trait to occur (Roff 1997). The first requirement is that there is genetic variation for alleles that control the trait of interest. If genetic variation exists there can be a phenotypic response to selection (the trait can evolve) as a result of changes in allele frequency.

In the context of FIE, fisheries often target the largest individuals in a population and the life-history attributes of these members of the population are removed (Policansky 1981, Williams and Shertzer 2005). Systematic removal of segments of the population that share similar phenotypes has been termed “phenotype-based selection” (Coltman et al. 2003). Size-selective rates of fishing mortality can be intense in commercial fisheries. Ricker (1981) estimated that 80% of two-year-old pink salmon are harvested each year by a fishery. Instantaneous fishing mortality exceeds 1.0 yr⁻¹ for many stocks, including Engraulidae, Sciaenidae, Bothidae, and Pleuronectidae species (Mertz and Myers 1998). Such intense selection imposes a de facto selective breeding program on the population: individuals that remain in the population have greater relative fitness than those harvested in the fishery.
The final condition for trait evolution is that the trait must be heritable: the genetic information that determines the expression of a phenotypic trait must be transmissible. The quantitative genetic metric of heritability in the narrow sense ($h^2_n$) is defined as the ratio of the additive genetic variance to the total phenotypic variance (Roff 1997) and quantifies the degree to which a trait is under additive genetic control that responds readily to selection. When heritability approaches zero, the trait is influenced completely by non-additive genetic and environmental effects. Values of $h^2_n = 1$ indicates complete additive genetic control of expression of the trait. Heritability values for wild marine fish populations are difficult to estimate because of environmental and temporal variability, overlapping generations, and long generation times. Heritability estimates for morphological, behavioral, and life-history traits measured in the laboratory are generally non-zero (Stokes and Law 2000) and may provide good estimates of the magnitude of heritability in the field (Weigensberg and Roff 1996). Life-history traits are expected to show low heritability because they are expected to be at an evolutionary equilibrium, and to have very little additive genetic variation remaining (Fisher 1930), or because they are subject to high environmental variation (Price and Schluter 1991). Although the relationship of the underlying genotype and observed phenotype is generally not well understood (Reed and Frankham 2001), phenotype is determined by underlying Mendelian inheritance. That such changes may be heritable, regardless of their potential to be reversed (Conover et al. 2009), indicates that ecological compensatory effects of removal may not always ameliorate the genetic effects of removal of some phenotypes.

The alteration of the frequency of phenotypes has implications for population dynamics: as selection works to remove some phenotypes, the corresponding life-history strategies of these individuals are also removed. Individuals maximize their fitness through expression of their
unique individual combination of growth and reproduction. Because resources are finite, it is not possible to maximize all morphological, behavioral, and life-history processes that increase fitness simultaneously, and hence individuals must make trade-offs in allocation decisions through ontogeny (Law 1979, Partridge and Harvey 1988). The alteration of phenotypes by selection and the resulting changes in population dynamics highlight the need to maintain phenotypic variability in populations in order to maintain sustainability (Allendorf et al. 1987). In the case of Atlantic cod and North Sea plaice, the phenotypes removed by harvest are those that exhibit delayed reproduction and high investment in early somatic growth (Rijnsdorp 1981, Barot et al. 2004, Ernande et al. 2004). These phenotypic changes are undesirable in a fishing management context (Conover and Munch 2002) because of the increased prevalence of phenotypes that exhibit reduced size-at-age.

In this study, I use a manipulative experimental approach to determine the realized heritability for length- and weight-at-age for a commonly used laboratory organism, Japanese medaka (*Oryzias latipes*). In addition to examining patterns of length-at-age of lineages exposed to multiple generations of length-specific removal for multiple generations, I describe patterns of life-history characteristics that contribute to individual fitness (age- and length-specific reproductive output) that would be of interest to managers interested in conserving yield. These findings have implications for the effects of size-selective removal, such as commercial fishing, on populations.
MATERIALS AND METHODS:

Broodstock and husbandry

The broodstocks of Japanese medaka used for this investigation were obtained from the Faculty of Science, Niigata University, Niigata, Japan (n = 63) and from a commercial source, Carolina Biological Supply, in the United States (n = 120). Fish were reared to reproductive age, and offspring from each generation were interbred for two generations. The fish were maintained at the Freshwater Mollusk Conservation Center at the Virginia Polytechnic and State University, Blacksburg, Virginia, USA in a multi-tank recirculating aquaculture system consisting of twelve 75.7-L tanks and a central 1000-L collection tank. Water was circulated to each tank at a rate of 13.1 L min⁻¹. Water was from a well and from treated municipal water and was maintained at 26.5°C (± 2.2°C SE) using submersible aquarium heaters (Appendix 2.1). Water quality was maintained with biological filtration and mechanical filtration, a 40-W UV filter, and frequent water changes. The light cycle was maintained in each tank using an 18-W fluorescent lamp controlled to cycle 14 hours of light and 10 hours of dark each day. Each tank was covered with black plastic to seal it from external light sources. Tanks were cleaned once every 1 to 2 days to remove feces and uneaten food. Tanks that held fish younger than 60 dph (days post-hatch) had outflows fitted with 2.54-cm (1-inch) foam filters to minimize mortality of juveniles. At ages of approximately 60 dph, the foam filter was removed and replaced with a strainer. All fish were fed two to three times daily. Fish less than 30 dph were fed with Zeigler® larval diet (≥ 40% protein, < 100 μm). Individuals 30 dph or older were fed with ground Aquatic Ecosystems® tropical flake food (≥ 40% protein). Diet was supplemented with live brine shrimp, administered every seven to ten days.
Experimental measurements and manipulation

Experimental manipulations of twelve Japanese medaka lineages were conducted in order to determine the heritability of length- and weight-at-age (total length, TL mm at 75 dph) and the response of somatic characteristics (growth rate from age 30 to 60 dph and the weight-length relationship) and reproductive characteristics (egg size and daily egg production) to directional length-specific removal over multiple generations (Figure 2.1). Each lineage was initiated, at generation one (G1), with approximately 300 randomly selected same-age larvae from the eggs produced by the F2 generation of broodstock. Thereafter, length-specific removal was performed at three treatment levels that consisted of removing 80%, 40%, or 0% (control) of individuals with the greatest TL.

For G1, and for each subsequent generation in a lineage, I measured somatic and reproductive characteristics at 15-day intervals to age 120 dph. Somatic growth measurements included the TL in mm and mass in g of a subset of at least 30 randomly selected individuals in each treatment. The total length of individual fish of ages 30, 45, and 60 dph was determined by digital image analysis. Images of known-age individuals were obtained by placing them in a shallow tank over a grid of known scale and taking a picture with a digital camera (5.0 megapixels). The image then was analyzed using the program Image Pro-plus (version 6.1, Media Cybernetics, Inc., Bethesda, MD, USA). The total length of each individual was determined by converting the number of pixels to millimeters using the scale of the grid system as a reference. Japanese medaka 60 to 120 dph were measured with calipers every 15 days. Individual mass was determined with a digital balance. To avoid incidental mortality, only fish 60 dph to 120 dph were weighed every 15 days. Female reproductive characteristics were quantified and included the daily number of eggs (clutch size) produced by a single female
(known weight, age, and TL) and the volume (mm$^3$) of eggs in that clutch. Egg collection and measurement was performed opportunistically. Upon detection of fecund females in a treatment, eggs in each clutch were collected directly from females. Japanese medaka retain their egg masses externally in tight clusters on the ventral area of their bodies until they deposit them on the substrate. Eggs were removed, counted, and measured by digital image analysis. The estimated radius of each egg was used to calculate spherical volume.

Length-specific removal was performed when individuals in a particular population attained age 75 dph. Individuals in that replicate were measured, and in accordance with the a priori treatment assignment established at G1, a proportion of individuals were removed from the population. That is, for the 80% removal treatment, the largest 240 individuals with respect to TL were removed from the replicate; for the 40% removal treatment, the 120 largest individuals were randomly removed and an additional 120 random individuals were removed. In the control treatments 240 randomly selected individuals, with respect to TL, were removed. Thus, the number of individuals in each replicate, after removal, was 60. The remaining individuals in each linearge served as the broodstock for the subsequent generation in that lineage. Eggs were collected for each replicate both directly from females and from loose, unattached eggs from the bottom of each tank, from broodstock aged 90 to 120 dph. This range of ages represents the peak fecundity for the broodstock; collection of eggs during this time was necessary to ensure an adequate number of eggs to start the next generation for each lineage, because the mortality through ~30 dph was near 60%. Offspring from each replicate were reared from egg to reproductive age to provide the broodstock for the next cohort, which were then subject to the same magnitude of size-selective fishing intensity as their parents.
Data analysis

Heritability was determined for length- and 75-dph weight. The realized heritability for a trait among generations in the same lineage was calculated by dividing the response to selection ($R$) by the selection differential ($S$). The selection differential was determined as the difference between the mean value of the phenotypic trait for the entire population and the mean value of the trait for those individuals selected from the population:

$$S = \mu_{\text{population}} - \mu_{\text{selected}}.$$

The response ($R$) of a phenotypic trait to selection, between generations, is the difference in the mean value of the phenotypic character among populations of succeeding generations:

$$R = \mu_{\text{population, } t=i} - \mu_{\text{population, } t=i+1}.$$

The variable $\mu_{\text{population, } t=i}$ is the mean trait value of the parents, and $\mu_{\text{population, } t=i+1}$ is the mean trait value of the offspring. Differences in the mean trait values among generations are a proportion of the selective differential. The response of the trait value to the selective process is used to estimate the heritability of the trait using the Breeders equation (Falconer and Mackay 1996):

$$h^2 = \frac{R}{S}.$$

Repeated measures analysis of variance (ANOVA) models were used to test whether differences in mean somatic growth characteristics and measures of egg production varied among treatments and generations. I tested whether the mean value of the 75-dph length and 75-dph weight in each treatment, prior to culling, differed significantly ($\alpha = 0.05$) among treatments and tested also for the presence of a significant interaction in weight- and 75-dph length among the four generations of the experiment. Similarly, repeated measures ANOVA was used to test whether significant differences in the magnitude of daily egg production, measured as the total
number of eggs collected from a clutch, or the mean size of eggs differed among treatments and
generations. ANOVA also was used to test for a significant interaction in the mean value of the
dependent variables, egg number and egg size, over generations.

Somatic growth characteristics (linear growth from age 30 dph to 60 dph and weight-at-
length) were determined. Model estimates were determined for all replicates in each treatment
(the greatest number of parameters) and for all replicates combined (the most parsimonious
model). The two alternative model formulations for each somatic growth characteristic were
tested using an $F$-test.

Linear growth was determined using least-squares regression of TL (mm) and age for
individuals in each treatment (age 30 to 60 dph) using the model:

$$TL = \beta_0 + \beta_1 \times \text{age (dph)}.$$  

I assumed that the residual error was normally distributed, which was verified qualitatively for
model fitting to each data set (replicate) using quantile-quantile (QQ) plots. Weight-at-length
was described with a two-parameter power function for each treatment:

$$W = aL^b,$$

where $W$ is an individual’s wet weight (g) and $L$ is an individual’s length (TL, mm). I assumed
that the residual error was log-normally distributed and verified normality of the error
qualitatively for each data set (replicate) examined using QQ plots. The 95% confidence
intervals (CI) of the model parameters ($a$, $b$) and ($\beta_0$, $\beta_1$) were determined empirically by fitting
an ellipse corresponding to the 95% probability region determined by the covariance of the
bivariate normal distribution of the parameters. The covariance matrix was determined by
repeated fitting ($n = 10,000$ trials) of the model to bootstrap samples (sampled with replacement)
of the observed data.
The mean range of maternal age at which eggs were detected and the range of numbers of eggs produced at this time were analyzed for all replicates combined for each treatment in each generation.

RESULTS:

Although the experiment was initiated with 12 lineages divided equally among the three harvest levels, only a fraction of these lineages persisted over four generations. Because of the inability to rear the number of individuals necessary to initiate the next generation (target \( n = 300 \)), some lineages were terminated during the course of the study. One generation, generation two, exhibited high juvenile mortality and the target number of individual in each treatment was not reached (Appendix 2.2). Although a majority of the lineages were able to be maintained it was not possible to determine ages of maturation for this generation.

The selection differential on 75-dph length, i.e., the difference in the mean length (mm, TL) of the removed individuals from that of the entire population, exerted on the replicates was as much as \(-6.70\) mm from the mean TL (Figure 2.2a). Over all replicates combined, selection resulted in a mean heritability estimate of the 75-dph length of 0.44 (95% CI = \(-0.149\) to 1.73, \( F = 7.01, R^2 = 0.41, P = 0.026 \)). The mean value for estimated heritability for 75-dph length was positive and significantly different from zero. In concert with the direct length-selective removal, I determined the extent to which an incidental selective response was observed in the value of 75-dph weight and found a similar positive, and significant, estimate of heritability for the mean 75-dph weight, 0.43 (95% CI = 0.235 to 0.615, \( F = 29.9, R^2 = 0.66, P = 0.027 \)) (Figure 2.2b).
The somatic growth relationships examined, weight-at-length modeled by the power function and linear growth rate of individuals from 30 to 60 dph, were variable in their response to length-specific removal (Figure 2.3a, b). However, the observed changes, though consistent among replicates in each treatment, were not significant. For each of these analyses, the reduced model formulations (i.e. the most parsimonious models) provided the best model fit as determined by $F$-test ($p >> 0.05$). These analyses indicated that there were no significant differences in model parameters for somatic growth following length-selective removal over generations or among treatments. The observed patterns in the mean value of the power function parameters $a$ and $b$ for two replicates in both of the 40 and 80% removal treatments over the course of four generations exhibited a decrease in the magnitude of the parameter $b$, the exponent, and a corresponding increase in the value of the coefficient parameter $a$ (Figure 2.3a). The magnitude of decrease in the exponent model parameter was greatest for the two treatments in the 80% removal replicate. No changes in power function parameters for the lineages in the control treatment were observed. The mean linear growth parameters $\beta_0$ and $\beta_1$ were negatively correlated ($R = -0.96$) (Figure 2.3b) and there were qualitative differences in the distributions of the $\beta_0$ and $\beta_1$ parameters among generations, especially for the 80% removal treatment.

Analyses performed to assess whether changes in mean values of growth characteristics, both somatic and reproductive, revealed insignificant results. Repeated measures ANOVA of the mean length (mm TL) and mean weight (g) of individuals age 75-dph prior to culling indicated that there was no significant ($\alpha = 0.05$) treatment effect, nor was there a significant interaction of treatment and generation number (Table 2.1a and b). The mean length at age 75-dph of all individuals during the course of the experiment, the “grand mean”, was 26.7 mm TL over four generations, and the grand mean of weight measurements was 0.24 g (Figures 2.4a and b).
Similarly, there was no difference in the size of removed individuals (culled individuals in the treatments following length-specific removal and random removal of individuals in the control) over the course of the experiment. Analysis of egg production of fecund females using repeated measures ANOVA indicated that there was no difference in the mean number of eggs produced by a female in a single clutch among treatments, nor was there a change in the mean number of eggs produced over the four generations examined (Table 2.2a). Similarly, there was no observed difference in mean egg size among treatments, nor did mean egg size change over the four generations examined (Table 2.2b). However, the temporal dynamics of egg production were altered significantly following length-selective removal (Figure 2.5). For the three generations examined—generations one, three and four—there was a significant reduction in the range of ages for which egg production was observed in the 80% removal treatment. Additionally, there was a reduction in the mean number of eggs collected from the last generation in the 80% removal treatment, but this reduction was not significant (α = 0.05).

DISCUSSION:

Studies of length-selective fisheries have suggested that fisheries-induced evolutionary processes alter growth and reproductive characteristics. However, these studies cannot offer controls or replication (McAllister and Peterman 1992a, b), nor can they falsify alternative hypotheses. In this study, I examined how somatic and egg-production characteristics of Japanese medaka populations maintained in the laboratory responded to length-selective removal over multiple generations. My experiment is conceptually similar to other manipulative approaches in the assessment of evolutionary responses of fishes in mesocosm and laboratory settings (Reznick 1990, Conover and Munch 2002, Conover et al. 2009). The results I report
indicate that, contrary to expectations, there were no detectable changes in mean length-at-age and weight-at-age over the four generations examined for either of the removal treatments relative to the control (Tables 2.1a and b). However, because of the frequency of measurements taken and the experimental design, I found significant changes in some somatic and egg-production characteristics for some replicates. Collectively, these results support the utility of manipulative selection experiments to further understanding of multivariate effects of directionally-selective process occurring in natural populations (Stearns 1984, Conner 2003). I suggest that these results can be used to understand contemporary evolutionary processes in length-selective fisheries.

The narrow-sense heritabilities estimated in this study were non-zero and indicate that directional selection altered the trajectory of somatic growth and demonstrated the presence of a mean phenotypic response to directional selection. Heritability in the narrow sense ($h_n^2$) is defined as the ratio of the additive genetic variance to the total phenotypic variance (Roff 1997). It is termed “narrow” because the index does not include genetic effects from dominance and epistatic interactions (non-additive effects within and between loci, respectively) (Falconer and Mackay 1996). Quantitative genetic measurements, such as narrow-sense heritability, can be obtained through the observation of the correlation of phenotypic traits between relatives (Falconer and Mackay 1996) and their estimation is best made through experimental manipulation; these methods reduce confounding factors and ease determination (Stearns 1984, Kempthorne 1997). In this study, I focused on the estimation of the morphological traits length-at-age and weight-at-age, as opposed to life-history traits, which have been defined as those traits that are “directly and invariably” associated with fitness such as fecundity and survival (Mousseau and Roff 1987). Although length-at-age has been shown to be correlated with
survival (Lorenzen 2000, Munch and Conover 2003), as are behavioral and physiological characteristics related to evolutionary fitness, I use the terminology presented by Mousseau and Roff (1987). The determination of heritability is of primary importance in plant and animal husbandry because it can be applied to predict the results of selective breeding programs, and thereby “improve” phenotypic traits of production interest (Hadley et al. 1991). The magnitude of heritability in the narrow-sense for length-at-age in selection experiments of Menidia menidia was estimated as 0.2 (Conover and Munch 2002). However, surveys of multiple studies examining heritability values of morphological traits of fishes indicated large variance in narrow-sense heritabilities for life-history and morphological characteristics (Tave 1993, 1995). The culling performed in this four-generation experiment was directed at altering the length-at-age; the resulting mean heritability estimated was nearly twice, but not significantly different from, the Conover and Munch (2002) estimate of −0.2 (mean $h^2 = 0.44$, 95% CI = −0.149 to 1.73). My study, however, had a much larger error associated with the mean $h^2$. The reduction in the number of replicates for each treatment through the course of the experiment (Figure 2.2) did not allow me to determine how heritability values may change over generations exposed to length-selective culling and decreased the precision of my mean heritability estimate. Quantitative genetics theory suggests that the additive genetic variance should become depleted over generations of selection and thus the realized heritability of traits would also be reduced (Roff 2002). I measured weight at the time of length-specific culling and observed a relatively large mean heritability value of 0.43, 95% CI = 0.235 to 0.615. It is possible that my results are positively biased because common rearing conditions reduced phenotypic variance (Roff 1997). Large variances, in part, may have resulted from non-assortative mating processes in the Japanese medaka (Howard et al. 1998, Koeski et al. 2000).
I did not find a difference in the mean length-at-age or weight-at-age of pre-culled populations among treatments or generations, and there were no interaction effects among treatments and generations (Table 2.1). This was an unexpected result because the heritabilities estimated for these morphological characters were non-zero. However, heritability is estimated as the slope of the linear regression of data from measurements of individual weight- and length-at-age, and the regressions exhibited a generally poor fit to both of the data sets ($R^2_{\text{length-at-age}} = 0.41$ and $R^2_{\text{weight-at-length}} = 0.66$). That is, the regression masked variation of each distribution and hence the ANOVA assessing differences in the point estimates of these traits were not significant (Table 2.1a and b). The characteristics of the medaka population and the experimental design may have contributed to the observed within-treatment variance, and reduced experimental power to detect differences in mean length-at-age and weight-at-age (Figure 2.4). The length-at-age and weight-at-age of the pre-culled individuals in the first generation indicated that a large amount of variation among replicates was present. Previous studies have utilized experimental culling have manipulated populations taken from the wild (Reznick 1983, Reznick 1990, 1997, Conover and Munch 2002) and my study may have been compromised by the limited inbreeding of historically allopatric stocks (Takehana et al. 2003, Takehana et al. 2004). Although I was able to maximize morphological variation prior to the initiation of the experiment, this approach may have compromised the ability to detect changes in mean point values for length-at-age and weight-at-age in the population. The intensity of length-selective harvest in my experiment may not have been enough to direct morphological evolutionary changes; previous studies of Atlantic cod, North Sea plaice and grayling fisheries and experimental manipulations (Haugen and Vøllestad 2001, Olsen et al. 2005, Rijnsdorp et al. 2005) had larger populations, and the culling
mortality equaled or exceeded mine. I conclude that our treatment effects did not alter the morphological point estimates of pre-cull length-at-age and weight-at-age.

I did not observe significant changes in somatic growth characteristics, nor did I observe significant changes among treatments or generations for the allometric growth relationships weight-at-length and linear early growth (age 30 to 60 dph) (Figure 2.3a and b) using an F-test. The power function relationship is commonly used to model the weight-at-length relationship (Quinn and Deriso 1999). I plotted the mean values of the distributions of the bivariate normally distributed parameters $a$ and $b$ from the weight-at-length regression and found that there were no significant changes in the distributions of the parameters in any of the control replicates, nor was there a pattern of parameter change in these replicates over the generations examined. In the 80% and 40% removal treatments, however, there were multiple replicates that exhibited patterns of decrease in the magnitude of the exponent parameter $b$ and in increase of the coefficient parameter $a$. The monotonic decrease in the exponent parameter over generations was especially large for the $b$ parameter in the 80% removal treatment. The absence of such a pattern in the control is notable. As an effect of the size-selective harvest, medaka may have been altering their morphology; specifically, the increase of the $a$ parameter and decrease in the $b$ parameter suggests that the fish were becoming increasingly elongated over the generations and less deep-bodied (Froese 2006). The weight-length relationship is indicative of individual condition, and alteration of this trait can affect reproductive capacity and subsequent population dynamics (Ventresca et al. 1995). Similar patterns of parameter change describing morphological alteration were observed in the early growth trajectories of the population in the experiment.

Because of the large variation in the length-weight relationship and the need for length data that extends to ages older than 120 dph (Leaf Chapter One), it was not possible to model
ontogenetic growth using the Von Bertalanffy growth function, the most commonly used growth model to describe length-at-age (Cailliet et al. 2006). However, linear models have been used to describe the growth of fishes in some life-stages. My investigation of the treatment effects on early linear growth rates indicated that no significant changes in this character occurred as a result of length-specific culling over generations or among treatments. However, in a similar analysis to that of weight-length, I did observe some changes in the pattern of the mean parameter values (Figure 2.3b): specifically, the magnitude of change in the slope parameter was greatest in the 80% removal treatment over the four generations examined. The decrease in the growth rate in this treatment and the lack of such a change in the control treatment indicate that length-specific removal may have had an effect on the early growth trajectory. A decrease in the early growth rates of individuals (i.e., the slope of the linear relationship) was negatively correlated with the intercept value, \( \beta_0 \). As the analysis of the length-weight relationship indicated a change in the morphology of fishes exposed to size-specific culling the analysis of linear growth rates, and the initial estimated size at age zero, the \( \beta_0 \) parameter, indicates that there may have been an alteration of early growth dynamics as well. The magnitude of \( \beta_0 \) may be related to the extent of maternal investment in eggs (Gagliano and McCormick 2007), which is inversely related to egg production in Japanese medaka (Leaf Chapter One), or to maternal age (Berkeley et al. 2004). Life-history theory suggests that changes in timing and alteration of the schedule of fitness-related processes, such as the onset of reproduction, will occur as other fitness related traits are altered (Roff 1992, Roff 2002). My observation of changes in size at zero dph (\( \beta_0 \)) in replicates of the removal treatments indicates that there have been changes in maternal resource allocation and these changes may be an effect of change in the timing of reproduction.
Although I did not observe a significant decrease in egg number or individual egg size (Table 2.2a and b), I did observe a significant decrease in the mean age over which reproduction occurred across generations for the 80% removal treatment (Figure 2.5). The observation of the significant change in the age of reproduction for the 80% removal treatment is an example of the “inadvertent” effects of directional selection (Abrams and Rowe 1996, Haugen 2000, Heibo and Magnhagen 2005). Such changes in the timing of the ages of maximum reproduction may be related to the observed pattern of change in the somatic growth relationship – these patterns, although not significant, indicated that an effect of size-selective removal is being manifested as a change in reproductive traits. Alternatively, just as length-selective removal resulted in non-zero heritability for 75-dph weight, length-selective removal may have removed those females, in the 80% removal treatment, with early maturation schedules.

Landmark studies have described heritabilities of life-history traits of harvested fish (Ricker 1981) and the evolutionary implications of length-selective fishing (Conover et al. 2005). In this study I show that fitness-related processes can be effected by length-selective removal even in the absence of detectable differences in length- and weight-at age. The consideration of changes in length-at-age is valuable in a fisheries management context, but other fitness-related traits and additional morphological, life history, and behavioral traits may be effected by length-selective removal. The effects are likely taxa specific and more work is needed to understand phenotypic trait correlations in a management context.
LITERATURE CITED:


Table 2.1. Repeated-measures ANOVA of a.) the mean length (mm TL) and b.) mean weight (g) of individuals age 75 dph prior to culling.

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<th>MSE</th>
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<th>$P$</th>
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Table 2.2. Repeated measures ANOVA of a.) daily egg production (the total number of eggs collected from a clutch) of fecund females and b.) mean egg size of collected eggs.

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Figure 2.1  Design of Japanese medaka culling experiment. The offspring of the founding population served to populate four lineages (illustrated by the stacked boxes) in each of three treatments. The target population prior to culling was 300 individuals. White solid arrows describe the culling regime (random removal and length-selective removal) for each treatment prior to offspring (egg) collection. The black solid arrows represent the offspring of the breeding population in each lineage that populate the succeeding generation in each lineage.
Figure 2.2. Plot of the relationship of the response (R) to selection (S) for A) mean length-at-age and B) weight-at-age of consecutive replicates of the same lineage. Individuals were age 75 days post-hatch (dph) at the time of selection.
Figure 2.3. Mean A) weight-at-length power function parameters ($a$ and $b$) for replicates from each generation and B) linear growth rate parameters (slope, $B_1$ and intercept, $B_0$) of individuals, 30 to < 75 dph. Arrows indicate direction of parameter value change among generations (labeled) for each replicate. Arrows indicate the direction of changes in parameter values, based on 95% bivariate normal confidence region.
Linear growth function parameter $B_0$

B

Linear growth function parameter $B_1$
Figure 2.4. Mean A) weight (g) of individuals (age 75 days post-hatch, dph) and B) length (TL, mm) of individuals (75 dph) from replicates in each treatment. The horizontal gray line is the grand mean age 75-dph weight and length, the average of all fish measured in the experiment.
Mean length (mm, TL) at age 75 days post hatch

Control

40%

80%
Figure 2.5. Mean age of egg production (days post-hatch) and mean number of eggs produced in a single clutch in each of the three generations (generations one, three, and four). Generation numbers are labeled. Vertical and horizontal error bars are the 95% confidence intervals.
Appendix 2.1. Temperature data recorded from sump tank recorded during the Japanese medaka culling experiment.
## Appendix 2.2. Number of individuals in each replicate prior to size-specific removal.

The target number of individuals in each replicate was 300.

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Chapter 3.

Evolutionary processes of length-selected populations: Validation of hypotheses using individual-based model simulation models

ABSTRACT:
Length-selective removal of individuals from natural populations has been identified as a cause of evolutionary selection and is suspected of altering their phenotypic composition. Experimental work has shown that sexual and somatic characteristics can be altered by phenotype-targeted removal. In this study, I constructed individual-based simulation models and qualitatively analyzed their ability to describe observed patterns in the biological characteristics of Japanese medaka under experimental length-selective culling. The model incorporates demographic and quantitative genetic processes. I found that the selectivity values of 75-dph (days post hatch) length did not differ among the candidate models, but that the estimate of the selection differential for 75-dph length was underestimated. The incorporation of the selection differentials of each of the candidate simulation models predicted the alteration of growth patterns observed of the various treatments and was contingent on the intensity of selection. Repeated measures ANOVA of the simulated population values of the length-at-age 75 dph and weight-at-age 75 dph changed significantly over generations and treatments (P < 0.05) for levels of heritability equal to 0.10, 0.20, and 0.30. These patterns contrasted those observed in the experimental manipulation. The candidate simulation models were poor at describing the observed changes in length- and age-at-maturity. The validation of models, constructed using information derived from laboratory data, life-history theory and quantitative genetic theory, is a first step toward
understanding the effects of selective processes in natural fish populations exposed to length-selective culling.

INTRODUCTION:

Selective processes serve as agents of evolution by controlling the distribution of phenotypes in populations (Darwin 1859). Although the tempo and intensity of selection are not well understood (Hoekstra et al. 2001), a variety of selective processes (e.g., directional, disruptive, sexual) are thought to interact dynamically (Kingsolver and Pfennig 2007). Contemporary evolutionary processes occur over short time periods, are driven by directional selection, and are increasingly widespread in human-impacted systems (Carroll et al. 2007). Examples of human-induced selective processes include pathogen control in medicine and agriculture (Williams and Nesse 1991, Palumbi 2001, Nesse and Stearns 2008), habitat alteration, and harvest of natural populations (Ricker 1981, Coltman et al. 2005, Waples et al. 2008). In the case of commercial harvest, length-selective removal has been identified as an agent of selection and is suspected of altering phenotypic composition (Ashley et al. 2003, Birkeland and Dayton 2005).

Because of the correlation of morphological and life-history characteristics that define schedules of somatic growth and reproduction, the effects of selection act simultaneously on multiple traits (Birkeland and Dayton 2005). In the case of fisheries-induced evolution individuals that are removed from populations share similar life-history characteristics. Such characteristics include length-at-age and increase their susceptibility to harvest. This increased susceptibility to harvest has consequences on the distribution of correlated traits. The pattern of phenotypic response is often illustrated/predicted using the Euler-Lotka equation, which
describes the mean expected lifetime production of female offspring ($R_0$), a measure of fitness, in a demographically stationary population (Stearns 1989, Beverton 1992, Stearns 1992, Roff 2002):

$$R_0 = \sum_{x=0}^{\infty} l_x m_x .$$  \hspace{1cm} \text{Equation 1}

In Equation 1, the value of $l_x$ is the probability of survival of an age-$x$ individual and $m_x$ is the age-specific production of female offspring. The structure of the Euler-Lotka equation allows ways by which $R_0$ can be maximized by varying the relative values of age-specific effects (Roff 2002). In the case of fishes, reproduction is strongly correlated with length, weight, and age. The Euler-Lotka equation can be re-written as:

$$R_0 = \sum_{x=0}^{\infty} l_x \left( \frac{L_x}{2} \right)^d ,$$  \hspace{1cm} \text{Equation 2}

where the age-specific production term in Equation 1, $m_x$, is replaced by variables that describe egg production as a power function based on an individual’s length-at-age, $L_x$ and the exponent, $d$. Offspring in this formulation are assumed to have a 50:50 sex ratio. Assuming that age-specific mortality, $l_x$, is constant, $R_0$ can be maximized by reducing $\alpha$, increasing length-at-age, increasing $d$, or all of these. An organism with unlimited resources and an infinitely plastic phenotype could maximize $R_0$ without having to make tradeoffs in allocation of somatic and sexual growth. However, such “Darwinian demons” do not exist and individuals must make allocation decisions throughout ontogeny (Kozlowski and Wiegert 1986, Parker and Smith 1990). Life-history theory suggests that there are strategies for maximizing fitness, but that the relationship of somatic and reproductive growth is predictable (Williams and Shertzer 2005). A population subject to length-selective culling results in an increased probability to remove individuals that have the potential to attain large lengths (Law 1979). Because resources are
finite, individuals may delay reproduction (increasing $\alpha$) or decrease the magnitude of length-specific egg production (reduce the power function exponent, $d$). Conversely, individuals that remain in the population are those that have reduced susceptibility to length-selective fishing and, on average, reduce their investment in somatic growth in favor of earlier maturation (decreasing $\alpha$) or increasing the power function exponent, $d$.

Although life-history theory provides a way to predict individual patterns of somatic and sexual development within generations, evolution is a process that occurs across generations. In order to predict the magnitude of expression of phenotypic characters over multiple generations there must be a link between the phenotype and selection: the trait must be under some degree of genetic control. Quantitative genetic analysis of phenotypes allows the determination of the degree of genetic control of a trait (its heritability) and prediction of how this trait will respond to selective pressure. The change in the mean value of a phenotypic characteristic between offspring and parents as a result of selection is termed the response to selection:

$$\Delta \mu = \mu_{\text{parents}} - \mu_{\text{offspring}}.$$  \hspace{1cm} \text{Equation 3}

The parameter $\mu_p$ is the mean trait value of the parents and $\mu_o$ is the mean trait value of offspring. Differences in mean trait values among generations are a proportion of the within-generation selection differential. The response of the trait value to the selective process has been described using the breeder’s equation (Falconer and Mackay 1996):

$$\Delta \mu = Sh^2.$$  \hspace{1cm} \text{Equation 4}

$S$ is the within-generation selection differential (i.e., the mean of the magnitude of the trait in the entire population prior to selection and the mean of the trait value after selection). Hence, the response to selection is contingent on the magnitude of selection ($S$) and the value of heritability, $h^2$. One key measure of the degree of genetic control of a trait is $h_n^2$, the heritability in the
“narrow sense”. Narrow-sense heritability ranges from zero to one, and is defined as the ratio of the additive genetic variance to the total phenotypic variance. The narrow-sense value indicates to what extent a phenotypic trait is controlled by genetics. Heritability values approaching zero indicate that the trait is influenced only by non-additive and environmental factors. Narrow-sense heritability enables prediction of the phenotypic response to selection. Empirical studies that have determined the response to selection are valuable because they allow estimation of heritability, prediction, and evaluation of correlated life-history and morphological characteristics. Landmark experimental work on guppies (*Poecilia reticulata*) and Atlantic silversides (*Menidia menidia*) indicated that phenotypes are plastic, selection causes heritable changes in selected traits, and there are alterations in correlated life-history and morphological traits (Lynch and Walsh 1998).

A variety of age- and size-structured projection models can be used to describe biological phenomena and individual-based models are becoming an increasingly popular tool for this type of analysis (Grimm et al. 2006). Although some hurdles remain in their description, implementation, and data requirements, individual-based models are a valuable tool for understanding complex biological phenomena (Fahse et al. 1998, Grimm 1999, Grimm et al. 2006). Recent theoretical work provided a comprehensive framework for evaluation of individual-based models (Williams and Shertzer 2005, Gusset et al. 2009) where alternative hypotheses can be constructed and mechanistic relationships can be quantified.

In this study I construct individual-based simulation models to understand the complex biological processes observed in a manipulative study that analyzed the biological characteristics of replicated populations subjected to length-specific culling. Japanese medaka (*Oryzias latipes*) with the greatest total length (TL) were culled from lineages with varying intensities (i.e., at
three treatment levels) over four generations (described in Chapter 3). I formulated simulation models that served as competing and testable hypotheses that could be validated by comparison to the results of the experiment. Validation of models, constructed using information derived from laboratory data, life-history theory and quantitative genetic theory, is a step toward understanding the effects of selective processes in natural fish populations exposed to length-selective culling.

MATERIALS AND METHODS:

*Individual-based simulation model structure*

The simulation models presented in the following sections serve as alternative hypotheses to describe the observed patterns in the biological characteristics (somatic and reproductive) of Japanese medaka under a regime of length-selective culling. Each candidate model has common structural characteristics and is implemented using an individual-based model framework. The components are: model initialization, intra-generational projection, determination of the selection differential, and inter-generational projection. Candidate model characteristics and the description of the qualitative evaluation scheme used to validate models are described below.

*Model initialization*

Each simulation consisted of 1,000 replicate populations for each of three removal treatments. Each replicate population was composed of 300 individuals. Every individual was assigned unique somatic and reproductive life-history characteristics based on their non-linear somatic growth relationships (Table 3.1). I assumed that there are no differences in the morphology and life-history characteristics of females and males. Length-at-age and weight-at-
length parameters \((L_c, a, b)\) were assigned to each individual by drawing random samples from the empirically derived normal distributions of each set of parameters. Length-at-age was described with a two-parameter von Bertalanffy growth function:

\[
L_t = L_c \left(1 - e^{-kt}\right).
\]  

Equation 5

This non-linear regression describes total length (TL) at age \((L_t)\) as a function of age, expressed as dph or days-post-hatch (Table 3.1, \(n = 2,327\) measurements taken from 990 individuals, \(R = -0.98\)). The value of \(k\) was fixed in the simulation to its mean value, 0.0101 y\(^{-1}\). Weight-at-length was described using a two-parameter power function:

\[
W = aL^b. 
\]  

Equation 6

**Intra-generation projection**

75-dph length and 75-dph weight were determined for each individual (Equations 5 and 6). I estimated the daily instantaneous natural mortality, \(M\), of individuals in the aquarium using unpublished data provided by Steven Manning, Gulf Coast Research Laboratory (Appendix 3.1). The daily instantaneous mortality rate, \(M\) was estimated to be 0.0018. Because the probability of an individual in any replicate dying during the course of the experiment was very small, individual mortality was not included in the model.

**Determination of the biological selection differential**

Length-selective removal took place at three treatment levels and occurred when the fish in each replicate attain age 75 dph. In the 80% removal treatment, the 240 individuals with the greatest length in each replicate were removed. The 40% removal treatment consisted of the removal of 120 individuals with the greatest length and the random removal of 120 individuals
with respect to length. In the control treatment, 240 randomly selected individuals were removed from the replicate. Selection differentials \((S)\) were determined for biological characteristics in each replicate by finding the difference between the mean values of the biological characteristics before removal (the mean values of the biological characteristics for 300 individuals) and after selection (the mean value of the biological characteristics of the remaining 60 individuals in each treatment) (Equation 3). Three differential selection values were determined for each replicate. The first two differential selection values were calculated based on the length-at-age 75 dph and the weight-at-age 75 dph. The selection differential of the (VBGF) von Bertalanffy growth function parameter \(L_\infty\) also was determined.

**Inter-generation projection**

I used the breeder’s equation (Equation 4) to predict the magnitude of phenotypic traits of the offspring \((\mu_{\text{offspring}})\) based on those of the parents \((\mu_{\text{parents}})\) and the magnitude of \(h_n^2\) and the selection differential under each selective regime for each generation. I used a range of heritability values to determine the response to selection for each candidate model described below. The trait under selection in each model was \(L_\infty\). Offspring of parents in each generation had, as their mean value of this parameter the \(L_\infty\) value as modified by the selection differential and heritability values (Figure 3.1).

**Candidate models**

Models were constructed to describe the observed patterns from the experiments. Each model shared, at the model initialization, typical biological characteristics of Japanese medaka (Table 3.1) and each was structurally similar (Figure 3.1). Models differed in the determination
of the value of length-at-age (following the effect of alternative heritabilities for this trait) and
the age and size of reproduction (Table 3.3). Fishes exhibit indeterminate growth, described
using the von Bertalanffy growth function. The value of length-at-maturity, \( L_\alpha \), can be predicted
as a function of the individual growth rate (\( k \)), asymptotic length (\( L_\infty \)), and the mean
instantaneous mortality rate (\( M \)) across age-classes (Charnov 1993, Charnov and Skúladóttir
2000) to maximize reproductive output:

\[
L_\alpha = L_\infty \left( \frac{3k}{3k + M} \right).
\]

Equation 7

Similarly, the predicted age at maturity, \( \alpha \), that maximizes the value of \( R_0 \) in Equation 1, was
derived by Roff (1984) and Beverton (1992), assuming a constant mortality rate in the
population:

\[
\alpha = \frac{1}{k} \log \left( \frac{3k}{M} + 1 \right).
\]

Equation 8

Preliminary analysis of the relationship of length- and age-of-reproduction (Equation 7 and 8,
Figure 3.2) indicated that these life-history characteristics were sensitive to the von Bertalanffy
characteristics \( L_\infty \) and \( k \) as well as to the natural mortality rate.

**Qualitative comparison and validation**

Candidate models were constructed with the aim of reproducing the observed biological
response of Japanese medaka to laboratory manipulations by incorporating empirically derived
and theoretical relationships of the response of correlated life-history traits. A valid candidate
model must replicate the non-significant changes in weight- and length-at-age 75 dph and also
describe pattern of changes in the timing of sexual development (Table 3.2). Validation of
models was performed using qualitative comparisons to these patterns.
Results:

The observed biological responses included both somatic and reproductive traits. I observed a pattern in the selection differential that was related to the selection intensity, and this is the first acceptance criteria for a valid model. Simulated populations based on biological characteristics of Japanese medaka should display similar magnitudes of the selection differential for each treatment (Table 3.2). I found that the values of 75-dph length and 75-dph weight were indeed similar in magnitude to those observed in the size-specific culling experiment. In the simulation model, the estimated mean selection differentials of 75-dph length in the control treatments were no different from zero (−0.02 mm ± 0.08 S.D.), nor did it differ from the selection differential values observed in the laboratory experiment. The estimated mean selection differential values increased in magnitude to −2.11 mm (± 0.12 mm S.D.) and −4.64 mm (± 0.19 mm S.D.) for the 40 and 80% removal treatments, and were similar to those observed in the culling experiment (Table 3.2). Similar patterns were observed in the estimated selection differential for 75-dph weight: an increase in the magnitude of the selection differential with the intensity of selection. There was a difference between the selection differentials observed in the experiment and those estimated using the simulation model for each treatment. The estimated mean selection differentials from the simulation model were 0.001 g (± 0.001g S.D.), −0.04 (± 0.001 g S.D.), and −0.08 g ± 0.002g S.D.) for the control 40%, and 80% removal treatments respectively.

The incorporation of the selection differentials of each of the simulation models altered the growth patterns observed for the various treatments (Figure 3.3a and b). The intensity of selection determined the magnitude of the reduction in 75-dph length and 75-dph weight, but was mediated by the value of the heritability (Figure 3.4). This pattern of decrease in 75-dph
length and 75-dph weight was not observed in the culling experiment; in that experiment there were there no detectable decreases of these traits over the four generations examined.

The final acceptance criterion to evaluate the validity of a candidate model was its ability to predict the observed changes in the age of egg production observed in the culling experiment. I found significant changes in the age of first egg production across generations in the 80% removal treatment (Table 3.2). Neither candidate model was able to describe this pattern. Model 1 predicted a very small reduction in length-at-maturity. Thus, the greatest magnitude of change in $L_\infty$ occurred in the 80% removal treatment using a heritability value of 0.30, and resulted in an 11% reduction in 75-dph length. The reduction in the asymptotic growth parameter however, translated to a reduction in an age-of-reproduction of only five days (a 4% reduction over four generations of selection). Estimates from candidate model 2 predicted a greater relative decrease in the age of maturity for each of the removal treatments. The 8% mean decrease in the estimated age-at-maturity over four generations is the maximum estimated from the model (80% removal intensity treatment with an assumed heritability of 0.30).

**DISCUSSION:**

In this study I used life-history and morphological data from captive Japanese medaka in concert with life-history theory and quantitative genetic principles to validate competing candidate models used to predict the outcome of experimental manipulations of Japanese medaka. The results were equivocal. Some aspects of the candidate models performed well in describing the patterns observed in the culling experiment. However, some aspects of the candidate models were unsatisfactory and indicated that the model was flawed in some critical
aspects. The description of such relationships is critical to understand the effects that size-selective harvest has on the evolutionary trajectories of populations (Conover et al. 2005).

Although one aspect of the determination of the selection differential was successful, indicating promise for at least one structural component of the simulation model (the precision of the initialization of length-at-age), other aspects of the model lacked the ability to describe the evolutionary trajectories of the culling experiment. The selection differentials for age-75 dph length for the three treatment levels were based on the truncation of normal distributions and the length-at-age of both the simulated and experimental populations followed this distribution. The selection differential of 75-dph weight was underestimated in the simulation model. Weight-at-length parameters $a$ and $b$ (Equation 9) were allocated to individuals during initialization of each generation independent of the length-at-age characteristics. Because an individual’s phenotype is the expression of a multitude of trait correlations, it is possible, and perhaps even likely, that weight-at-length characteristics are not distributed independently in the population. Alternatively, the underestimation of the selection differential for 75-dph weight may indicate that these parameters have smaller variances than those used in the model. The underestimation of this selection differential is not trivial; it indicates that there are undiagnosed, latent relationships that are not accounted for in the model. The use of condition indices, of which the weight-length relationship is integral, can be used to better understand the effects of compensatory processes (Jakob et al. 1996). Ecological processes, such as physiological compensation, tend to reduce the evolutionary effects of size selectivity through the limitation of resource competition.

I found that even at low values of heritability, there were significant changes in length-at-age 75 dph and weight-at-age 75 dph among generations and treatments. The deterministic
nature of the simulation model, with respect to the constant heritability value, that relates phenotypic characteristics of successive generations may not be biologically realistic. Theoretically, there is only a finite source of genetic variance and hence a limit to phenotypic change (Gjedrem 1985). Even in highly controlled aquaculture situations, there are limits to genetic improvement (Hardy 1999). The assumption of constant heritability used in the model implies that selective effects are constant across generations. Because of the logistical difficulties that were encountered in the experimental manipulation, however, it was not possible to determine whether heritabilities were altered over generations. An experiment with a greater number of replicates, treatments, and individuals in each treatment will be necessary to explore this outstanding issue. A study that is able to describe the variation of heritability over generations would be valuable to furthering understanding of evolutionary processes caused by phenotypic selection.

An outstanding characteristic that neither of the candidate models was able to describe was the magnitude of decrease in the age of maturation, especially in the 80% removal treatment. I fixed the value of the von Bertalanffy growth parameter \( k \) and the instantaneous natural mortality rate, \( M \). Such assumptions are simplifications that likely compromised the ability of the model to describe the life-history patterns that I observed. In addition to the correlation of the von Bertalanffy growth parameters (Chen et al. 2003), there are other population-level correlations that can be incorporated into future modeling work. Specifically, there is a correlation between \( k \) and \( M \) (Roff 1992):

\[
M = 1.65k .
\]  

Equation 9

Efforts to increase model complexity will require additional assumptions. In this study I used population-level parameters to describe individual-based phenomenon. However assigning
individual parameters without knowledge of the complex relationships that underlie expression of the phenotype is perilous at best and spurious at worst. Although arduous, an empirical approach that uses tagged individuals may help to illuminate some of the outstanding complexities and physiological relationships that control the phenotype. In a complementary manner, population-level descriptions of the relationship of growth and natural mortality should be more fully understood. These efforts would serve to increase the complexity of models and also likely would improve their predictive power.

In this work, I used a qualitative approach to compare life-history and morphological characteristics of simulated and observed populations. Qualitative approaches to link complex models to experimental data have been used with success (Shertzer et al. 2002) and represent a necessary step for understanding complex ecological and evolutionary behavior. Regardless of the methods used to evaluate model validity, alternative modeling approaches can be used. Models that use bioenergetic (Leonard and Robertson 2005) and molecular (Elena and Lenski 2003) approaches to understanding evolutionary change could be especially informative.
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Table 3.1. Summary of quantitative analyses of life-history and morphological traits of Japanese medaka *Oryzias latipes* performed in this study. Age presented as dph (days post-hatch) and length is mm total length (TL)

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Model</th>
<th>Model name</th>
<th>Estimated parameter values (mean ± 95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length-at-age</td>
<td>$L_t = L_\infty (1 - e^{-kt})$</td>
<td>2-parameter VBGF</td>
<td>$L_\infty = 50.7$ mm TL (48.6 to 53.7 mm TL) $k = 0.00947$ dph$^{-1}$ (0.0087 to 0.010 dph$^{-1}$)</td>
</tr>
<tr>
<td>Weight-at-length</td>
<td>$W = aL^b$</td>
<td>Power curve</td>
<td>$a = 2.16 \times 10^{-5}$ (1.77 $\times 10^{-5}$ to 2.55 $\times 10^{-5}$) $b = 2.79$ (2.73 to 2.84)</td>
</tr>
</tbody>
</table>
Table 3.2. Patterns of the selection differential and age of egg production observed in the experimental removal.

It was not possible to estimate the age of reproduction for generation two because of large mortality in every replicate of the experiment.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>80%</th>
<th>40%</th>
<th>0%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selection differential</td>
<td>-5.36 (0.96)</td>
<td>-2.97 (0.60)</td>
<td>0 (0.99)</td>
</tr>
<tr>
<td>75-dph length mean (S.D.)</td>
<td>-0.12 (0.03)</td>
<td>-0.09 (0.01)</td>
<td>0.05 (0.005)</td>
</tr>
<tr>
<td>Age of egg production, range (mean age dph) ± 95% CI</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Generation One</td>
<td>101 to 124</td>
<td>78 to 130</td>
<td>77 to 170</td>
</tr>
<tr>
<td>Generation Two</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Generation Three</td>
<td>71 to 113</td>
<td>88 to 113</td>
<td>106 to 112</td>
</tr>
<tr>
<td>Generation Four</td>
<td>30 to 65</td>
<td>75 to 111</td>
<td>72 to 114</td>
</tr>
</tbody>
</table>
Table 3.3. Summary of candidate model used to describe the observed phenotypic characteristics and life-history traits in the Japanese medaka *Oryzias latipes* removal experiment. Variables in the model, $k$ dph$^{-1}$ and $L_\infty$ mm, are the von Bertalanffy growth function parameters.

<table>
<thead>
<tr>
<th>Number</th>
<th>Model Name</th>
<th>Selection pressure</th>
<th>Heritability value ($h^2$)</th>
<th>Reproduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Length-specific reproduction</td>
<td>$L_\infty$</td>
<td>0.1</td>
<td>$L_o = L_\infty \left( \frac{3k}{3k + M} \right)$</td>
</tr>
<tr>
<td>1.2</td>
<td></td>
<td></td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>1.3</td>
<td></td>
<td></td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>2.1</td>
<td>Age-specific reproduction</td>
<td>$k$</td>
<td>0.1</td>
<td>$\alpha = \frac{1}{k} \log \left( \frac{3k}{M} + 1 \right)$</td>
</tr>
<tr>
<td>2.2</td>
<td></td>
<td></td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>2.3</td>
<td></td>
<td></td>
<td>0.3</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.1. Flow chart of simulation model.
Figure 3.2. Expected relationship of A) age-at-maturity (days) and B) length-at-maturity (TL, mm) related to von Bertalanffy growth function parameters and instantaneous annual mortality rate.
Figure 3.3. Trajectories (n = 1,000 replicates) of mean somatic growth over four generations for control (black solid line), 40% (black dashed line), and 80% removal (gray line) for: A) 75-dph length and B) 75-dph weight. The heritability value used in the simulation was 0.2.
Figure 3.4. Trajectories (n = 1,000 replicates) of somatic growth over four generations at three levels of heritability and a selection intensity of 80% removal. Heritability values are 0.10 (black solid line), 0.20 (black dashed line), and 0.30 (gray line) for: A) 75-dph length and B.) 75-dph weight.
Appendix 3.1. Results of an unpublished study to monitor natural mortality of Japanese medaka populations (population sizes were 30 to 35 individuals) maintained in aquaria. Data used for analysis were estimated from graphical data provided by S. Manning, Gulf Coast Research Laboratory. Four replicates are displayed (gray dashed lines). The expected natural mortality, using an exponential decay model was calculated by least-squares estimation. The best fit line is displayed with a solid black line. The percent remaining in the population is $\% = e^{-Mt}$, where $M$ is the daily mortality rate, 0.0018 day$^{-1}$ and $t$ is the age of the individual, in days.
Chapter 4.

An individual-based simulation model to explore the effects of length-selective fishing on an age-structured population

ABSTRACT:

Phenotype-based selection by commercial fishing is increasingly recognized as a cause of morphological and life history changes in harvested populations. In this work, I simulated the biological characteristics of an age-structured population exposed to length-selective harvest in order to evaluate changes in morphology, the von Bertalanffy growth function (VBGF) parameter $L_\infty$, and to determine how change in morphology alters the size structure of the population and fishery characteristics, as measured by yield- and egg-per-recruit metrics. The model is initialized with 400,000 individuals, each having unique somatic and sexual characteristics based on empirically derived data from Atlantic cod $Gadus morhua$ and allocated into twenty age-classes. The population was projected for 40 years, and the annual effect of fishing was characterized by measuring the annual selection differential (the difference in the mean value of $L_\infty$ between fished and unfished populations). The selection differential was incorporated into the VBGF growth characteristics of age-one recruits. I found that the selection differential for all levels of instantaneous fishing intensity examined ($F = 0.2, 0.4, \text{and } 0.6 \text{ y}^{-1}$) was non-zero drove the reduction of the $L_\infty$ value of recruits over the 40-year projection. The reduction in $L_\infty$ truncated the size distribution and reduced yield- and egg-per-recruit. The inclusion of a slot limit, reducing the precision in targeting individuals at the minimum size limit, and modeling the population with length-specific natural mortality rates all reduced the selection differential and minimized fishery-induced morphological changes. Though the magnitude of the selection differential was sensitive to biological and fishery dynamics, the magnitude of change
of morphological characteristics, even at low levels of fishing mortality, was non zero. The results presented here provide information to fisheries managers interested in implementing management policies that reduce morphological changes in harvested populations.

INTRODUCTION:

There have been increasing awareness and concern of the effects of harvest on targeted populations (Law 2007, Kuparinen et al. 2009). In addition to reducing biomass and altering the age structure of populations, a topic receiving increasing attention is the evolutionary change observed, termed fishery-induced evolution (FIE) (Eikeset et al. 2005, Hutchings and Fraser 2008). FIE processes alter the life-history and morphological characteristics of individuals, resulting in changes in the dynamics of populations (Ratner and Lande 2001). That heritable phenotypic, or evolutionary, changes occur due to harvest has been documented in a range of species (Coltman et al. 2003, Sharpe and Hendry 2009). Such work indicates that harvested populations may not be as resilient as previously assumed: dynamic changes in biological characteristics may reduce the totality of compensatory ecological mechanisms (Myers et al. 1995, Shelton and Healey 1999, Bowers and White 2002). Thus, management strategies that balance both genetic and demographic processes with the demands of harvest may be desirable. Such “evolutionarily enlightened” management would recognize the value of intraspecific variation that is necessary for maintaining variation of those traits beneficial for yield and resilience (Ryman et al. 1995) and would acknowledge the rapidity of evolutionary change (Heino 1998, Ashley et al. 2003).

Evolutionary effects that occur over the course of a human lifetime, such as FIE, are referred to as “contemporary” evolutionary effects (Hendry and Kinnison 1999) and are similar
to long-term evolution in that they are determined by two conditions: the presence of a selection differential on a phenotypic trait and genetic control of that trait (Roff 1992). The selection differential is a metric that quantifies the difference between the mean value of a phenotypic trait in a population exposed to selective processes, such as that imposed by length-selective fishing, and that in an identical, unfished population. Changes in phenotype, in the context of harvest management, are the result of fishing mortality (harvest) exacted on individuals in a population that are similar in one or more continuous phenotypic traits (such as size-at-age or timing of spawning). The exhibition of these traits by one component of the population increases their susceptibility to harvest (Coltman et al. 2005). Those individuals that remain in the population then have greater fitness relative to those that are harvested. In order for the short-term ecological changes in a population exposed to directional selection to have long-term evolutionary effects, the selected traits must be heritable: they must be under genetic control to some extent. The magnitude of genetic control can be described by the index \( h^2 \), termed the “narrow-sense heritability” which ranges from zero to one. Heritability values of zero indicate that the magnitude of trait expression is under complete environmental control and non-zero values indicate that there is some degree of genetic control of the trait; \( h^2 = 1 \) indicates that the magnitude of trait expression is completely controlled by genetic processes (Falconer and Mackay 1996). Heritability estimates for morphological, behavioral, and life-history traits measured in the laboratory are generally non-zero (Stokes and Law 2000), but are generally small for morphological traits (Mousseau and Roff 1987, Falconer and Mackay 1996).

The alteration of the frequency distribution of phenotypes of individuals has implications for population dynamics. Different phenotypes maximize their fitness in different ways: an individual has the ability, subject to genetic and developmental constraints (Gould and Lewontin
1979), to allocate resources in an effort to maximize survival and reproductive output. Because resources are finite, an individual must make trade-offs in allocation decisions (Roff 1983, 1984). It is the individual differences in resource allocation, expressed as a phenotype, that result in individual differences in survival and reproductive growth.

The individual-based simulation model structure is well suited to quantitative genetic and demographic investigation because of its ability to model biological characteristics at an individual level and observe the “bottom-up” population-level phenomena that result (Grimm 1999). Although there are some drawbacks to using individual-based models, specifically an increase in model complexity over age- or stage-based algorithms that makes communication of model structure difficult (Grimm et al. 2006), they do allow great flexibility. Because of their inherent flexibility, they are an increasingly popular way to investigate complex phenomena in the biological and social sciences (Grimm et al. 2006). The objective of the model developed in this study is to better understand evolutionary processes acting on harvested fish populations and identify the biological characteristics and management strategies that hasten such phenomena.

In this model, I begin with the premise that morphological traits, such as asymptotic length, are heritable. I describe, using an individual-based model of a simulated age-structured population of Atlantic cod *Gadus morhua*, the changes in asymptotic length that occur as a result of length-selective fishing. The selection differential is calculated annually and the phenotypic response is incorporated into the characteristics of offspring mediated by the magnitude of the heritability index. Williams and Shertzer (2005) used an individual-based simulation model to describe patterns of intra-annual selection for a single year, and I build on their work. The goal of this work is to determine how individual growth characteristics of a simulated population respond dynamically to a given management strategy. Specifically, I determine the magnitude of
the selection differential on a morphological trait (asymptotic length) for a range of biological and fishery management characteristics. I then describe how the value of asymptotic length varies in the population over the course of the multi-year projection and describe how changes in asymptotic length, an individual phenotypic characteristic, alter yield- and egg-per-recruit values (YPR and EPR) of the population.

**MATERIALS AND METHODS:**

I used individual-based simulation models to follow the fate of individuals in two identical populations over multiple generations; one population was exposed to length-selective fishing mortality and natural mortality during a single year, and the second population was exposed only to natural mortality. Populations were projected in two components (Figure 1). The first component was structured to determine the value of the intra-annual selection differential, $S$. The intra-annual selection differential was the difference in the mean value of the phenotypic trait of interest of the fished ($\mu_{\text{fished}}$) and unfished ($\mu_{\text{unfished}}$) populations following the assessment of mortality during a single year:

$$S = \mu_{\text{fished}} - \mu_{\text{unfished}}.$$  

(1)

The second component incorporated the value of the intra-annual selection differential, $S$, to determine the phenotypic composition of offspring ($\mu_{\text{offspring}}$):

$$\mu_{\text{offspring}} = \mu_{\text{unfished}} + Sh^2.$$  

(2)

The mean value of the phenotypic trait of the offspring was based on the selection differential, the magnitude of heritability ($h^2$), and the mean of the phenotypic character of interest in the unfished population($\mu_{\text{unfished}}$) (Falconer and Mackay 1996).
Population structure and biological characteristics

The simulation was initialized with 400,000 females distributed among 20-age classes (longevity, \( \omega = 20 \)). Each individual was assigned to an age-class \( (j) \) following the relative probability defined by the exponential decay function:

\[
P_j = \frac{e^{-Mj}}{\sum_{j=1}^{\infty} e^{-Mj}}.
\]

Where \( M \) is the instantaneous natural mortality rate and equal to 0.2 y\(^{-1}\). To determine age class assignment, a uniform random number, \( \theta \) on [0,1], was drawn for each individual in the population. An individual, \( i \), was assigned to age class \( n \) if:

\[
\sum_{j=1}^{n} P_j < \theta_i \leq \sum_{j=1}^{n+1} P_j, \tag{4}
\]

If \( R_i < P_{j=1} \), the \( i^{th} \) individual was assigned to age-class one.

Somatic growth (length-at-age, and weight-at-age) and reproductive (length-specific egg production) characteristics were assigned to each individual. I modeled individual length-at-age using a two-parameter von Bertalanffy growth function (VBGF) (von Bertalanffy 1938, Ebert 1998):

\[
L = L_\infty \left(1 - e^{-kt}\right). \tag{5}
\]

Where \( L_\infty \) is the average length of the largest individuals in the population and \( k \) is the von Bertalanffy annual growth rate constant (y\(^{-1}\)). Each individual in the population was assigned a unique value of the VBGF parameter, \( L_\infty \), the only growth parameter that varied among individuals. The value of \( L_\infty \) for each individual was determined by taking random samples from the normal distribution defined by the published VBGF \( L_\infty \) values:
Normal($\mu_{L_{\infty}} = 101.8 \text{ cm}, \sigma_{L_{\infty}} = 12.1 \text{ cm}$) (Table 1). The value of $k$ was the same for each individual and was equal the mean of the published VBGF $k$ values, $0.18 \text{ y}^{-1}$ (Table 1). This value was used to predict the age at which $50\%$ of individuals in the population were mature ($A_{50}$) using the relationship (Beverton 1992):

$$A_{50} = \frac{3k + M}{k}. \quad (6)$$

Given the parameters $M = 0.2 \text{ y}^{-1}$ and $k = 0.18 \text{ y}^{-1}$, the estimate of $A_{50}$ was $7.27 \text{ y}$. The weight-at-length relationship was modeled with a power function:

$$W = aL^b. \quad (7)$$

I assigned identical values to the parameters $a$ and $b$ (0.01 and 3, respectively) to each individual.

A unique length-specific egg production parameter was assigned to each individual. This parameter was determined by modeling the published data for length-specific egg production with a power function (Table 1):

$$E = LC. \quad (8)$$

Individual values of $c$ ($c_i$) were determined by drawing random samples from the empirical distribution Normal($\mu_c = 4.03, \sigma_c = 0.10$) from the power function regression.

**Intra-annual simulation**

The selection differential ($S$) imposed on the growth parameter $L_{\infty}$, by length-selective fishing, was calculated as the difference in the mean value of this parameter for the breeding individuals of an unfished population (subject only to natural mortality) and a fished population (subject to both natural and fishing mortality):
\[ S = L_{\text{fished}} - L_{\text{unfished}}. \quad (9) \]

To determine the values of \( S \) in the model, the biological characteristics of each individual in the simulated population, derived above, were duplicated and analyzed in parallel (Figure 1).

The simulated, duplicated populations were projected in semi-annual time steps (Figure 1). At the beginning of each six-month period, natural mortality was imposed on individuals in each population at an annual rate of \( 1 - e^{-M} \) (equivalent to a six-month probability of death equal to \( 1 - e^{-\frac{M}{2}} \), or 0.095). For each individual, in both populations, a random number (\( \theta_i \)) was drawn from a uniform distribution on [0,1]. The individual was removed from the population if \( \theta_i \) was less than 0.095. The number of individuals that suffered natural mortality (\( N_M \)) in each population was recorded.

An individual was subject to fishing mortality if three criteria were fulfilled: (1) it was the fishing season, (2) it was selected for fishing (its length qualified it to be taken by the fishery based on the minimum size limit) and (3) it was harvested. In the fished population, the probability that an individual was selected for fishing was defined by the logistic probability distribution function (LPDF) (Hastings and Peacock 1975), which determined the length-specific (\( L_i \)) probability of susceptibility to harvest:

\[ P_{L_i} = \frac{1}{1 + e^{-\alpha(L_i - L_{50})}}. \quad (10) \]

The parameters of the LPDF (\( \alpha \) and \( L_{50} \)) defined the steepness of the logistic function and the length at which 50% of the individuals in the population were selected. The LPDF is commonly referred to as the selectivity curve. The value of \( \alpha \) in the simulation was 0.10. An individual’s susceptibility to fishing was determined by comparing a random number \( \theta_i \), drawn from a uniform distribution on [0,1], to \( P_{L_i} \). It was selected by the fishery if \( \theta_i \leq P_{L_i} \). The fished
population was subject to fishing mortality at a rate of $F \text{ y}^{-1}$. The probability of mortality, due to fishing, was equal to $1 - e^{-F}$. For each individual selected by the fishing gear ($\theta_i \leq P_{L_i}$), a random number ($\theta_i$) was drawn from a uniform distribution on [0,1]. The individual was taken by the fishery and removed from the population if $\theta_i \leq 1 - e^{-F}$. The number of individuals that were subject to fishing mortality ($N_{F}$) was recorded.

The second phase (2nd six months) of the intra-annual projection was the phase in which egg production occurred for both populations. For each individual in the population whose age exceeded $A_{50}$, the magnitude of monthly egg production was determined. The parent’s unique VBGF parameter, $L_{\infty_i}$, and the magnitude of its egg production were saved.

Every individual, in each duplicated population, aged and grew during the year. As individuals aged, they grew, and the magnitude of growth was based on the individually specified VBGF parameter, $L_{\infty_i}$ and $k$.

At the end of the year the selection differential was determined. Then, the mean value of the VBGF parameter $\bar{L}_{\infty}$ was determined for each duplicated population using a weighting scheme based on an individual’s total annual egg production:

$$w_i = \frac{E_i}{\sum_{j=1}^{n} E_j}, \quad (11)$$

$$\bar{L}_{\infty_{population}} = \frac{\sum w_i L_{\infty_i}}{\sum w_i}, \quad (12)$$

That is, because of the weighting scheme used to determine $\bar{L}_{\infty_{population}}$, only those individuals that produced eggs (the parents) contributed to the mean $L_{\infty}$ in each population. The selection
differential was calculated as the difference between the two population values of \( L_\infty \), where the population was either the fished or unfished population:

\[
S = L_\infty^{\text{fished}} - L_\infty^{\text{unfished}}. \tag{13}
\]

**Multi-year projection**

Quantitative genetic determination of phenotypic traits were implemented in the multi-year projection by incorporating the selection differential into the mean VBGF characteristic \( L_\infty \) of the offspring; their life-history characteristics reflected the intra-annual selective process acting on the parents. The response (\( \Delta \)) to selection is described by the breeders’ equation (Falconer and Mackay 1996):

\[
\Delta = Sh^2, \tag{14}
\]

and was incorporated into the growth characteristics of the offspring:

\[
L_\infty^{\text{offspring}} = L_\infty^{\text{parents}} + \Delta. \tag{15}
\]

I simulated a population of recruits (age = 1 year) that entered the population every year. The number of recruits \( N_R \) was equal to the number of individuals removed from the population from natural and fishing mortality, \( N_M \) and \( N_F \):

\[
N_R = N_M + N_F. \tag{16}
\]

Unique individual VBGF \( L_\infty \) values of recruits were determined by random sampling from the normal distribution defined by \( (\mu = L_\infty^{\text{offspring}}, \sigma_{L_\infty}) \) (from equation 15 and \( \sigma_{L_\infty} = 12.1 \text{ cm} \)). The somatic and reproductive characteristics of individual recruits were determined as described above. Thus, the fished population at end of the projection year \( t \) was composed of all of the individuals at \( t \) and the recruits (age one). The fished population was duplicated and analyzed in
the intra-year simulation: one duplicate was subject to both harvest and natural mortality and the other duplicate was subject only to natural mortality.

Analysis of population characteristics

The value of the selection differential, population age structure, and individual biological characteristics were determined for each year of the projection. The 40-year projection was repeated (a set of \( n = 25 \) iterations) and the mean estimate of the selection differential for each year was reported. For each set of iterations, the model was initiated using a unique combination of fishing intensity (\( F = 0.2, 0.4, \text{ or } 0.6 \text{ y}^{-1} \)) and length of entry into the fishery (\( L_{50} = 75, 85, \text{ or } 95 \text{ cm} \)).

I evaluated how changes in the mean VBGF parameter \( L_{\infty} \) of the population altered \( \text{YPR}_{\text{MAX}} \) and \( \text{EPR}_{\text{MAX}} \), the maximum yield- (Y) and egg- (E) per-recruit, for the mean population values of \( L_{\infty} \) observed in the simulation. \( \text{YPR} \) was calculated following the length-specific formulation reported by Chen (1997):

\[
\text{YPR} = \sum_{j=1}^{n} \left[ \frac{W_j P_j F}{P_j F + M} \left( 1 - e^{-P_j F - M \Delta T_j} \left( e^{-\frac{L_{\infty}}{k} (P_j F + M \Delta T_j)} \right) \right) \right]. \tag{17}
\]

Where \( W_j \) is the mean weight of an individual in the \( j \text{th} \) length class. The variable \( \Delta T_j \) is the duration (y) that an individual will remain in size-class \( j \) and is determined from the VBGF parameters (\( k \text{ y}^{-1} \) and \( L_{\infty} \text{ cm TL} \)), the width of the size-class (\( d = 5 \text{ cm} \)), and length of entry into the size-class (\( L \text{ cm TL} \)):

\[
\Delta T_j = \frac{1}{k} \log_e \left( \frac{L_{\infty} - L_j}{L_{\infty} - L_j - d_j} \right). \tag{18}
\]
The maximum egg-per-recruit value was determined using the length-based variant of the age-structured model presented by Prager et al. (1987) and followed the formulation presented by Chen (1997). Parameters in this model are similar to those of the YPR model, but include length-specific egg production \( E_j \) of the median-length individual in the \( j^{th} \) length-class:

\[
EPR = \sum_{j=1}^{n} \left( E_j e^{-\frac{1}{\sum_{k=1}^{j}(p_r + p_d)AT_k}} \right).
\]  

(19)

**Simulation scenarios**

In addition to altering the intensity of harvest \( (F \text{ y}^{-1}) \) and length of entry into the fishery \( (L_{50} \text{ cm}) \), I examined scenarios in which I altered model parameters singly: either the biological (genetic and demographic) or harvest characteristics of the fishery. Each model projection (40 years) was repeated (a set of \( n = 25 \) iterations) to estimate the mean selection differential for each year. I determined the mean value of the population \( L_\infty \) and the distribution (mean and standard deviation) of the lengths of individuals in each age-class at the termination of the 40-year projection. An explanation of what parameters varied in each scenario is listed here and summarized in Table 2. I used a heritability value of 0.2 unless the otherwise stated.

1.) The contribution to \( L_{\infty \text{offspring}} \). For each different year of the multiyear simulation, only 10, 20 and 50\% of randomly selected breeding individuals contributed to the value of \( L_{\infty \text{offspring}} \).

2.) The pattern of natural mortality was length specific. The initial population structure and the probability of natural mortality was calculated using the function:

\[
M_L = M_i \left( \frac{1}{L} \right),
\]  

(20)
where \( M_L \) is the annual instantaneous natural mortality rate of an individual fish length \( L \), TL cm. The parameter \( M_1 \) is a constant and is the instantaneous natural mortality rate of an individual with total length = 1 cm. The instantaneous mortality rate of a fish this size is equal 15 y\(^{-1}\) (Lorenzen 2000, 2005).

3.) The variance of \( L_\infty \). I altered the value of the variance of \( L_\infty \) in simulations: the CV of \( L_\infty \) was 1.2 or 1.4 times that of the base model. Additionally, I set the value of the variance of \( L_\infty \) to be proportional to a constant coefficient of variation (CV = \( \frac{\sigma_{L_\infty}}{\mu_{L_\infty}} \)).

4.) The value of the narrow-sense heritability, \( h^2 \). I examined biological characteristics of the population for alternative values of \( h^2 \), 0.1 and 0.3.

5.) Susceptibility of individuals to the fishery. A slot limit was imposed where only individuals within a size interval were harvested. Two slot limits were examined: 70 to 80 cm TL and 75 to 85 cm TL.

6.) The value of the steepness parameter of the selectivity curve. The value of \( \alpha \) was changed to 0.05 and 1.0.

I performed a simulation in which I examined the ability of the length-structured population to rebound, in the absence of fishing, following 40 y of harvest. Phenotypic rebound is the ability of the population to attain the mean value of \( L_\infty \) that it exhibited prior harvest. It was not possible to use the complete formulation of the simulation model for this investigation because the magnitude of the response to selection was contingent on selection pressure that becomes non-existent when \( F = 0 \) y\(^{-1}\) (equations 14 and 15). Hence, I started the rebound simulations with the biological characteristics and population structure after 40 y of harvest under a range of instantaneous fishing mortalities (\( F = 0.2, 0.4, 0.6 \) y\(^{-1}\)) and lengths of entry into the fishery (\( L_{50} = 75, 85, 95 \) cm TL). Populations were projected for 40 y with individuals.
recruiting to the population at the end of each year to replace the number lost ($N_{\text{M}}$) to natural mortality ($M = 0.2 \, \text{y}^{-1}$).

The individual growth characteristics of age-one recruits were determined by random sampling, with replacement, the VBGF parameter $L_\infty$ of reproductive adults. Sampling was weighted as a function of the total annual reproductive output based on an individual’s length-specific egg production. Once the mean VBGF parameter $L_\infty$ had been drawn, the normal distribution, $\text{Normal}(\mu = L_\infty, \sigma = \sigma_{L_\infty})$, was randomly sampled to determine the $L_\infty$ of each recruit. The remaining biological characteristics (weight-at-age, length-specific egg production, age at 50% maturity) were determined for each individual as described above.

RESULTS:

Simulated size-selective fishing exerted a non-zero selection differential on the age-structured population for all values of $F \, \text{y}^{-1}$ examined (Figure 2). The magnitude of the selection differential was at its maximum at the initiation of exploitation. Although the magnitude of the selection differential was reduced later, its value remained non-zero. Imposition of the non-zero selection differential reduced the mean value of the population $L_\infty$ and the yield over the projection for all levels of fishing mortality (Figure 3). The mean value of the population $L_\infty$ decreased linearly over time. Two processes acted to make this so: the imposition of the selection differential onto the growth parameters of recruits and the removal of those individuals with $L_\infty$ values sufficiently large to be exploited by the fishery. The initially large value in yield was a result of removal of individuals from the previously unexploited population. This population consisted of individuals with biological characteristics distributed randomly among age-classes. Following this initial peak, and depending on the intensity of fishing mortality, the
age-structure of the population became truncated, resulting in reduced yield during the bulk of the projection. The majority of the truncation and alteration of the distribution of lengths in the oldest age-classes occurred during the first ten years of fishery exploitation (Figure 4). The increase in yield at $t = 10$ to 12 years occurred as individuals in early age-classes were harvested by the fishery. The linear, monotonic decrease in yield after approximately 12 years was caused by the selection-induced changes in biological characteristics of the age-one recruits that eventually enter the fishery.

The value for the size of entry into the fishery had differential effects on the mean $L_\infty$ values within each age-class over the course of the projection (Figure 5) and resulted in reduction of the population mean $L_\infty$ value (Table 3). At the same level of fishing mortality, the length of entry determined the mean value of $L_\infty$ for each age-class. The smaller the length of entry into the fishery, the greater was the reduction of age-specific $L_\infty$. Earlier age-classes exhibited a decrease in mean $L_\infty$ because of the inclusion of age-one recruits with reduced values of $L_\infty$.

Altering the biological characteristics in various scenarios affected the magnitude of change of mean $L_\infty$ values relative to the base scenario values (Table 3). Changes in the mortality schedule and fishery characteristics (selectivity and the imposition of a slot limit) had the greatest impact on the net change in $L_\infty$. The inclusion of length-specific mortality served to decrease the natural mortality rate of large individuals, allowing their reproductive contribution to increase which in turn resulted in an increase in population $L_\infty$ for all levels of fishing mortality examined. The magnitude of increase diminished with greater fishing mortality. Alterations to the logistic parameter $\alpha$, of the fishing selectivity curve, altered the precision of harvest to target an individual of given length. Reduction of the steepness parameter ($\alpha = 0.05$)
reduced the precision of harvest and reduced the magnitude of change in $L_\infty$. Conversely, increasing the steepness parameter ($\alpha = 1.0$) increased the precision of the fishery and served to increase the magnitude of change in mean population $L_\infty$ by increasing the selection differential. The incorporation of a slot limit resulted in near-zero changes in population mean $L_\infty$ over the course of the simulation. Alterations in heritability, the inclusion of a lottery effect for reproductive contribution, and increasing the variance in $L_\infty$ had lesser impacts on the net change of $L_\infty$. The incorporation of a lottery effect, where the contribution of parents to the mean $L_\infty$ of the age-one recruits is a random sample of the possible contributors, resulted in a relatively small decrease in the mean population $L_\infty$. Increases in the variance of $L_\infty$ (to 1.2 and 1.4 times the coefficient of variation of $L_\infty$ in the base model) resulted in a small decrease in mean population $L_\infty$ values relative to the mean estimates. Alteration of the heritability value did not greatly alter the magnitude of change of $L_\infty$ values of the population.

Changing the biological characteristics of the population over the course of the projection affected YPR and EPR (Figure 6). As the value of $L_\infty$ increased, the maximum YPR increased was found at greater fishing mortality. Similarly, the larger the value of $L_\infty$, the greater was the maximum egg production of the population. The rate of increase in the maximum estimated YPR increased with larger lengths of entry into the fishery. In the case of the 95 cm TL entry into the fishery, the fishing mortality at which YPR was maximum increased and was at a plateau at $F = 0.57$ to 0.59 y$^{-1}$.

Phenotypic rebound was examined for simulated fishing moratoria. My results indicated that after forty years of suspension of harvest pressure, populations had not attained mean values of pre-harvest $L_\infty$ values (Table 4). Those simulations that had the least fishing pressure during harvest exhibited the greatest mean $L_\infty$ values, but less than 50% of the population reached pre-
harvest $L_\infty$. Simulated populations exposed to $F = 0.6 \, y^{-1}$ resulted in 32.9 to 39.0% of individuals meeting or exceeding the population pre-harvest $L_\infty$ value.

**DISCUSSION:**

In this study, I explored how the action of quantitative genetic processes altered biological growth characteristics in an age-structured simulated population subjected to length-selective harvest. Experimental work to describe the population effects of fishery-induced evolutionary changes on biological characteristics has been performed on single cohorts (Conover and Munch 2002, Conover et al. 2005, Conover et al. 2009) and simulation modeling has assessed the magnitude of the selection differential caused by fishing on an age-structured populations for a single fishing season (Williams and Shertzer 2005). However, for natural systems exposed to harvest, biological and demographic processes are dynamic, hence the work presented here is an attempt to understand how evolutionary dynamics act on age-structured populations over multiple generations. The results presented here imply that at low fishing mortalities ($F \geq 0.2 \, y^{-1}$), the magnitude of the selection differential is non-zero. If the expression of life-history traits is controlled to some extent by genetic processes and thus are heritable ($h^2 > 0$), then the population mean and age-class specific values of $L_\infty$ are reduced by length-specific fishing. I described the expected rate of decrease of mean $L_\infty$ under realistic biological and fishery conditions, explored the efficacy of alternative management strategies, and described the effects that alternative biological characteristics have on the population value of $L_\infty$. Such changes in the biological characteristics of populations resulted in alteration of YPR and EPR values.
The quantitative genetic effect of fishing, as measured by the magnitude of the observed selection differential, was most rapid at initial exploitation of the population (Figure 2). During this period, many large individuals in the population were available for harvest (Figure 4), and the population was comprised of individuals with the growth parameter $L_\infty$ distributed randomly with respect to age (Figure 1). For simulations with levels of fishing mortality greater than $F = 0.4 \text{ y}^{-1}$, the removal of individuals greater than the size of entry into the fishery was nearly total within a few years (Figure 3) and the largest decrease in mean $L_\infty$ within age-classes occurred during the first five years (Figure 5). The removal of individuals from the harvested population exacerbated the differences in $L_\infty$ among the populations: the only individuals remaining in the harvested population were those with (small) $L_\infty$ values that did not allow recruitment to the fishery. The increased reproductive success of these remaining, small individuals (in the absence of those removed by harvest) resulted in the initially large selection differential, $S$. In the latter years of the simulation, phenotype-based selection played a primary role in the determination of the selection differential. During this period, the population was fully exploited, the size structure was truncated, and the susceptibility of individuals to harvest was based on individual length as the result of their growth characteristics: only those individuals that had sufficiently large $L_\infty$ values to allow recruitment to the fishery were harvested; there were fewer of these individuals, and because they were harvested at the least size (and youngest age) possible, their contribution of gametes to the next generation, weighted by the length-specific egg production, was minimized.

I hypothesized that the effect of fishing (expressed as the response, $R$) was proportional to the intensity of fishing (manifested as the selection differential, $S$) through a linear relationship that is mediated by the value of narrow-sense heritability, $h^2$. Narrow-sense heritability
quantifies the degree to which a trait is under genetic control: when heritability approaches zero
the trait is influenced only by non-additive genetic and environmental effects. Generally, the
measurement of heritability ($h^2$) is defined as the ratio of the additive genetic variance, $V_a$, to the
total phenotypic variance (Roff 1997), where the total phenotypic variability, $V_p$:

$$h^2 = \frac{V_a}{V_p}.$$  \hspace{1cm} (21)

Strictly defined, this estimate of heritability is called “heritability in the narrow sense” because it
does not include genetic effects from dominance and epistatic interactions (non-additive effects
within and between loci, respectively) (Falconer and Mackay 1996). Heritability estimates for
morphological, behavioral, and life-history traits measured in the laboratory are generally non-
zero (Stokes and Law 2000) and may provide good estimates of the magnitude and direction of
heritability measured in the field (Weigensberg and Roff 1996). Experiments upon wild
populations of guppies (Poecilia reticulata) subjected to directional selection that was similar in
magnitude to that observed in nature exhibited rates of evolution of age and size-at-maturity
similar to those found in artificial selection experiments in laboratory settings (Reznick and
Ghalambor 2005). Heritability estimates of mean age-at-length of Atlantic silversides (Menidia
menidia) determined from length-specific removal experiments, were $0.198 \pm 0.02$. Heritability
values for morphological traits, such as growth, of wild marine fishes are difficult to estimate
because of environmental variability, overlapping generations, and long generation times. One
such attempt to measure heritability made use of the philopatry of anadromous Atlantic salmon
The heritability estimates for body weight of grilse (individuals that return after one year at sea)
ranged from 0.19 to 0.36. Against this background, my in deterministic projection model, I used
a narrow-sense heritability value of 0.2 for each year; however, genetic control of phenotypic
traits is not expected to be constant in a fluctuating environment, for a population that has experienced the reduction of phenotypic (and genetic) variation, and for populations subject to high rates of immigration. Alternative measures of heritability include the inclusion of terms that describe the interaction of environmental and genetic components and the role of maternal effects (Falconer and Mackay 1996). Regardless of the precise value of $h^2$, values greater than zero will result in an impact of the selection differential upon the biological parameters of age-one recruits. Non-zero selection differentials were apparent even as the size distribution in the population became truncated (Figure 4). The rate of decrease in mean $L_\infty$ values of recruits was reduced, but there remained a continual decline in mean population $L_\infty$ values (Figure 3), which resulted in the decrease in yield.

A difficulty for accurately simulating population response to size-selective fishing, and one that is nearly intractable, is how to estimate the limits of phenotypic plasticity. That harvested fish populations lose molecular genetic variation as a result of fishing has been documented (Jones et al. 2001, Quinn et al. 2001, Hauser et al. 2002), but the relationship between genetic and quantitative variation is not well understood (Reed and Frankham 2001). It is reasonable to assume that there are limits to the ability of populations to respond to perturbation. Environmental variation and selective processes both shape phenotype (Schlichting 1989) and may serve to limit or intensify the extent of harvest-induced selective processes. Because the limits of phenotypic variability are not well understood, it is not reasonable to project a population's response to harvest using my deterministic model indefinitely. Additive morphological variation would be exhausted at some time (Roff 1997), and it is not reasonable to project the population beyond the ~five generations (40 years) that I present here.
When the model parameters were altered the results were informative. The simulation analyses indicated that a slot limit, a sufficiently narrow range where harvest mortality is eliminated, ensured that most individuals in the population were able to breed, and resulted in a selection differential value that approached zero for all levels of fishing. Alternative management strategies, such as seasonal or other temporal closures, could ensure that each individual in the population has the opportunity to breed, and for a size-selective fishery it is expected that a minimum size limit may provide such a refuge. In my results as the length of entry into the fishery was increased the selection differential was decreased. Protecting a component of the population is an effective strategy to maintain phenotypic variation in the fished population (Table 3). However, because of the intensity of fishing examined (up to three times natural mortality) decreases in mean $L_\infty$ were still apparent. My results indicated that a more precise harvest operations increased the selection differential. Increasing the precision of harvest just above the minimum size limit is desirable to reduce growth overfishing and to ensure that a minimum amount of egg production is maintained. The slot limit that I examined is a harvest strategy that does not alter growth characteristics and should be considered by managers attempting to minimize the evolutionary effect of fishing. However, fishing is likely to affect several morphological and life-history traits simultaneously because of the genetic correlation of somatic and sexual growth traits to schedules of mortality and reproduction (Stearns 1989, Beverton 1992, Williams and Shertzer 2005). The effects of life-history tradeoffs among phenotypes in the context of size-selective harvest have been documented: size-selective fishing is thought to be the cause of reduced size and age at maturity for Atlantic cod (Gadus morhua) and North Sea plaice (Pleuronectes platessa) (Grift et al. 2003, Olsen et al. 2004, Olsen et al. 2005). Because I did not attempt to model the covariance of life history traits, the simulation I
present is conservative (i.e., no changes in the maturity or mortality schedules were incorporated that would serve to hasten phenotypic change).

The differential alteration of the population $L_\infty$ values that I reported in the simulation scenarios indicates that the selection differential is sensitive to perturbation of some model parameters. Although the instantaneous natural mortality of fish populations often is assumed to be near 0.2 $y^{-1}$, the incorporation of a natural mortality rate that decreases with length is reasonable. The incorporation of size-specific mortality to some degree reverses the pattern of the fishery-induced selection differential because the mortality of large individuals in fished and unfished populations is greatly reduced. Individuals in these populations have the ability to contribute, at each time period, to the biological characteristics of offspring. For the unfished population, the contribution from many ‘large’ individuals, even those with relatively small $L_\infty$ values, effectively swamps the contribution of individuals with larger $L_\infty$ values. Changes in the parental contribution had very little effect on the selection differential and resulting patterns of mean $L_\infty$ model because the genetic contribution of even 10% of the mature individual provides an accurate sample of mean population values. Analysis of molecular genetic markers has shown that large populations of marine fishes generally have very small genetically effective population sizes; i.e. small numbers of individuals contribute to the genetic composition of offspring (Hoarau et al. 2005, Poulsen et al. 2006). The inclusion of sampling an even smaller percentage of the population likely would result in a projection that would exhibit large temporal variability in the selection differential.

Simulation analyses play are necessary to explore of the subject of fishing-induced evolution. A variety of confounding hypotheses have been invoked to explain the decline and lack of recovery in some fished populations (Chouinard 2002), and it is probably the case that a
multiplicity of environmental and biotic factors contribute to persistence of populations at low levels. Assessing fishery-induced evolutionary processes is difficult for wild populations (McAllister and Peterman 1992b, a, c) and studies of laboratory and mesocosm experiments, though necessary, are unsatisfactory in some ways because they lack the complexity of natural systems. The simulation results that I present indicate that heritable changes in morphology and life history have the potential to affect length-at-age of individuals over generations. Although the magnitude of the selection differential is sensitive to biological and fishery dynamics, the rate of change in $L_\infty$ is contingent on the value of heritability. Although the value of heritability is difficult to measure in the field, the combination of positive values for heritability, in concert with non-zero selection differentials will result in changes in offspring morphology that are contrary to the goals of fishery management and conservation.
LITERATURE CITED:


Table 4.1. Biological parameters used in the base model.

### Weight-at-age

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<tr>
<th>Parameter</th>
<th>$a$</th>
<th>$b$</th>
<th>$n$</th>
<th>Sex</th>
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<th>Source</th>
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<td>3.094</td>
<td>9145</td>
<td>Baltic ICES SD 22</td>
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</table>

### Length-specific egg production

<table>
<thead>
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<th>Length (cm, TL)</th>
<th>Egg production (x 10$^7$)</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>37.5</td>
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<td>Captive-reared, Norwegian coast</td>
<td>Kjesbu et al. 1996</td>
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<td>67</td>
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<td>50</td>
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<tr>
<td>49</td>
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<tr>
<td>50</td>
<td>0.48</td>
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<tr>
<td>72</td>
<td>2.87</td>
<td></td>
<td></td>
</tr>
<tr>
<td>63</td>
<td>1.83</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.1 continued.
Length-specific egg production

<table>
<thead>
<tr>
<th>Data</th>
<th>Length (cm, TL)</th>
<th>Egg production ( \times 10^7 )</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>68</td>
<td>1.52</td>
<td>Captive-reared Norwegian coast</td>
<td>Kjesbu et al. 1996</td>
<td></td>
</tr>
<tr>
<td>72</td>
<td>1.93</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>63</td>
<td>3.01</td>
<td></td>
<td></td>
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</tbody>
</table>

Length-at-age

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Linf (cm, TL)</th>
<th>k (( y^{-1} ))</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>116.0</td>
<td>0.10</td>
<td>Baltic</td>
<td>FishBase.org</td>
<td></td>
</tr>
<tr>
<td>120.0</td>
<td>0.13</td>
<td>Baltic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>106.0</td>
<td>0.18</td>
<td>Baltic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>95.4</td>
<td>0.16</td>
<td>Baltic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>96.6</td>
<td>0.17</td>
<td>Baltic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>108.0</td>
<td>0.15</td>
<td>Baltic</td>
<td></td>
<td></td>
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<tr>
<td>112.0</td>
<td>0.15</td>
<td>Baltic</td>
<td></td>
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<tr>
<td>103.0</td>
<td>0.15</td>
<td>Baltic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>116.0</td>
<td>0.11</td>
<td>Canada Grand Bank</td>
<td></td>
<td></td>
</tr>
<tr>
<td>110.0</td>
<td>0.11</td>
<td>Canada Gulf of St. Lawrence</td>
<td></td>
<td></td>
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<tr>
<td>90.6</td>
<td>0.24</td>
<td>Canada ICNAF 1B</td>
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</tr>
<tr>
<td>87.0</td>
<td>0.31</td>
<td>Canada ICNAF 1B</td>
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<td>101.0</td>
<td>0.13</td>
<td>Canada ICNAF 3L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>102.0</td>
<td>0.16</td>
<td>Canada ICNAF 3L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>83.9</td>
<td>0.25</td>
<td>Canada ICNAF 3L</td>
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<tr>
<td>98.0</td>
<td>0.15</td>
<td>Canada ICNAF 3M</td>
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<td>124.0</td>
<td>0.12</td>
<td>Canada ICNAF 4</td>
<td></td>
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<td>115.0</td>
<td>0.10</td>
<td>Canada ICNAF 4T</td>
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<td></td>
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<tr>
<td>78.0</td>
<td>0.25</td>
<td>Canada ICNAF Pn</td>
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</tr>
</tbody>
</table>
### Table 4.1 continued.

**Length-at-age**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Linf (cm, TL)</th>
<th>k (y⁻¹)</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>110.0</td>
<td>0.15</td>
<td>Iceland E</td>
<td></td>
<td></td>
</tr>
<tr>
<td>102.0</td>
<td>0.23</td>
<td>Iceland SW</td>
<td></td>
<td></td>
</tr>
<tr>
<td>98.5</td>
<td>0.39</td>
<td>Irish Sea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>98.8</td>
<td>0.28</td>
<td>New England USA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>123.0</td>
<td>0.23</td>
<td>North Sea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>95.9</td>
<td>0.28</td>
<td>Norway Lofoten Islands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>105.0</td>
<td>0.13</td>
<td>Norway North Sea</td>
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<td></td>
</tr>
</tbody>
</table>
Table 4.2. Simulation scenarios explored by perturbation of model parameters.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parental contribution</td>
<td></td>
</tr>
<tr>
<td>Lottery 10%</td>
<td>$L_{\infty, \text{offspring}}$ is randomly determined from a fraction of eligible parents.</td>
</tr>
<tr>
<td>Lottery 20%</td>
<td></td>
</tr>
<tr>
<td>Lottery 50%</td>
<td></td>
</tr>
<tr>
<td>Mortality schedule</td>
<td></td>
</tr>
<tr>
<td>$M_L = M_1 \left( \frac{1}{L} \right)$</td>
<td>Size-specific instantaneous natural mortality rate is length-specific $M_1 = 15L^{-1}y^{-1}$.</td>
</tr>
<tr>
<td>Variance of $L_\infty$</td>
<td></td>
</tr>
<tr>
<td>$CV L_{\infty} = 1.2 \times \text{Base}$</td>
<td>Increase CV by 1.2 and 1.4</td>
</tr>
<tr>
<td>$CV L_{\infty} = 1.4 \times \text{Base}$</td>
<td></td>
</tr>
<tr>
<td>$CV L_{\infty} = 11.8%$</td>
<td>Fixed CV</td>
</tr>
<tr>
<td>Heritability</td>
<td></td>
</tr>
<tr>
<td>$h^2 = 0.1$</td>
<td>Alter the magnitude of the narrow-sense heritilbity.</td>
</tr>
<tr>
<td>$h^2 = 0.3$</td>
<td></td>
</tr>
<tr>
<td>Impose a slot limit</td>
<td></td>
</tr>
<tr>
<td>Slot limit (70 to 80 cm, TL)</td>
<td>$F = 0,y^{-1}$ for individuals not in this size interval.</td>
</tr>
<tr>
<td>Slot limit (75 to 85 cm, TL)</td>
<td></td>
</tr>
<tr>
<td>Change fishery selectivity</td>
<td></td>
</tr>
<tr>
<td>$\alpha = 0.05$</td>
<td>Alter the steepness of the logistic probability distribution function that determines fishery selectivity.</td>
</tr>
<tr>
<td>$\alpha = 1.0$</td>
<td></td>
</tr>
</tbody>
</table>
Table 4.3  Mean population $L_\infty$ (cm TL) at the conclusion of the simulation (and the percent change in mean population $L_\infty$ from the start to the end of the simulation). The Base simulation uses the biological and fishery characteristics described in the text. In each simulation, biological and fishery characteristics are altered singly.

<table>
<thead>
<tr>
<th>Simulation scenario ($L_{50} = 75$ cm TL)</th>
<th>$0.2$</th>
<th>$0.4$</th>
<th>$0.6$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base</td>
<td>106.0</td>
<td>108.7</td>
<td>110.5</td>
</tr>
<tr>
<td>% Parent contribution 10</td>
<td>97.1  (-4.5%)</td>
<td>93.9  (-7.4%)</td>
<td>92.0  (-9.3%)</td>
</tr>
<tr>
<td>% Parent contribution 20</td>
<td>97.0  (-4.5%)</td>
<td>94.1  (-7.3%)</td>
<td>92.0  (-9.2%)</td>
</tr>
<tr>
<td>% Parent contribution 50</td>
<td>97.1  (-4.5%)</td>
<td>94.2  (-7.2%)</td>
<td>92.0  (-9.2%)</td>
</tr>
<tr>
<td>Mortality schedule Length-dependent mortality</td>
<td>117.7  (15.2%)</td>
<td>116.3  (14.0%)</td>
<td>115.0  (12.9%)</td>
</tr>
<tr>
<td>Coefficient of variation of $L_\infty$ 1.2 x base</td>
<td>95.6  (-5.9%)</td>
<td>91.7  (-9.7%)</td>
<td>88.9  (-12.3%)</td>
</tr>
<tr>
<td>Coefficient of variation of $L_\infty$ 1.4 x base</td>
<td>94.1  (-7.4%)</td>
<td>89.0  (-12.3%)</td>
<td>86.1  (-15.1%)</td>
</tr>
<tr>
<td>Coefficient of variation of $L_\infty$ Proportional to mean</td>
<td>97.3  (-4.3%)</td>
<td>94.5  (-6.9%)</td>
<td>92.6  (-8.6%)</td>
</tr>
<tr>
<td>Heritability $h^2 = 0.1$</td>
<td>97.4  (-4.2%)</td>
<td>95  (-6.4%)</td>
<td>93.4  (-7.9%)</td>
</tr>
<tr>
<td>Heritability $h^2 = 0.3$</td>
<td>97.4  (-4.1%)</td>
<td>94.9  (-6.5%)</td>
<td>93.1  (-8.1%)</td>
</tr>
<tr>
<td>Slot limit 70 to 80 cm TL</td>
<td>101.7  (-0.1%)</td>
<td>101.8  (0.0%)</td>
<td>101.7  (-0.1%)</td>
</tr>
<tr>
<td>Slot limit 75 to 85 cm TL</td>
<td>101.7  (-0.1%)</td>
<td>101.9  (-0.1%)</td>
<td>101.8  (0.0%)</td>
</tr>
<tr>
<td>Fishery selectivity $\alpha = 0.05$</td>
<td>98.2  (-3.4%)</td>
<td>95.7  (-5.7%)</td>
<td>94.0  (-7.3%)</td>
</tr>
<tr>
<td>Fishery selectivity $\alpha = 1.0$</td>
<td>95.7  (-5.7%)</td>
<td>92.1  (-9.3%)</td>
<td>89.8  (-11.4%)</td>
</tr>
</tbody>
</table>
Table 4.4. Percent of population with $L_{\infty}$ values less than 101.8 cm TL (the mean popuation $L_{\infty}$ prior to fishing) after a 40-year fishing moratorium.

<table>
<thead>
<tr>
<th>$F$</th>
<th>$L_{50}$ cm TL</th>
<th>75</th>
<th>85</th>
<th>95</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.2</td>
<td>44.0</td>
<td>42.8</td>
<td>44.9</td>
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</tr>
<tr>
<td>0.4</td>
<td>36.4</td>
<td>38.7</td>
<td>40.9</td>
<td></td>
</tr>
<tr>
<td>0.6</td>
<td>32.9</td>
<td>35.3</td>
<td>39.0</td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.1  Flow chart of simulation model. AFR is the age at which the first reproductive event occurs. VBGF is the von Bertalanffy growth function.
Figure 4.2. Mean value of the selection differential ($S$, cm) for each annual iteration of the forty-year projection for three lengths of entry ($L_{50}$ is the length [cm, TL] at which 50% of individuals of that size enter the fishery) and four levels of instantaneous fishing mortality, $F = 0.2$ (filled circle), 0.4 (open circle), 0.6 (filled square), and 1.0 $y^{-1}$ (open triangle).
Figure 4.3. A.) Mean population $L_\infty$ for the base-model projection in the simulation, and B.) Mean harvest yield (kg) for each year of the projection with a length of 50% entry into the fishery, $L_{50} = 75$ cm TL and four levels of instantaneous fishing mortality, $F = 0.2$ (open triangle), 0.4 (filled circle), 0.6 (open square), and 1.0 y$^{-1}$ (filled triangle).
Figure 4.4. Length-frequency distribution for each of 20 age-classes over the duration of the projection (years 1, 5, 10, 20, and 40) for the base model simulation, $L50 = 75$ cm TL and $F = 0.4$ y$^{-1}$. Increasingly older age-classes are displayed with lighter shades of gray.
Figure 4.5. Distribution of mean $L_\infty$ for each age-class over the duration of the projection (years 1, 5, 10, 20, 30, and 40 are displayed in increasingly lighter shades of gray and are labeled on the left side figure).
Percent of maximum yield-per-recruit and egg-per-recruit (black line) and $F_{\text{max}} y^{-1}$ (gray line) for a given mean population $L_\infty$ value (represented as TL cm and as the percent change in length from the mean $L_\infty$ of the base model at the start of the projection). Note that the percent maximum EPR occurs at $F = 0 y^{-1}$.