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Density-dependent life history compensation of an iteroparous salmonid

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Contents

DENSITY-DEPENDENT LIFE HISTORY COMPENSATION OF AN ITEROPAROUS SALMONID

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Abstract.

We examined the response of life history traits in a heavily overexploited population to a 28-fold change in density after the removal of harvest mortality. Density-dependent changes in both growth and survival were observed. As life history theory predicts, this had repercussions for reproductive life history characteristics. Increased density caused a delay in maturation and increased the frequency of skipped reproductive events, primarily by individuals of poor condition. However, size-at-maturation and the proportion of fish skipping reproduction differed between the sexes suggesting that life history tradeoffs differ among the sexes. The rapid response of these life history traits to changes in density suggests that these changes were primarily due to phenotypic plasticity, although the importance of natural and artificial selection should not be discounted. The magnitude of the variation in the traits represents the degree to which the population was able to compensate for overharvest, although the overexploited state of the population at the beginning of the study demonstrates it was not able to fully compensate for this mortality. However, no evidence of depensatory processes was found. This in combination with the plasticity of the life history traits has important implications for the resilience of the population to overharvest. Furthermore, density-dependent growth may have the unintended result of making size-based regulations less conservative at low levels of population abundance, as younger fish, perhaps even immature fish, become vulnerable to harvest. Finally, the variation in life history traits in relation to evolutionary change is discussed. Results from this study demonstrate the importance of considering not only survival, but also changes in life history characteristics for management and conservation.

Key words: phenotypic plasticity; skipped spawning; maturation; growth; fecundity; recovery; fisheries management; recreational fishing; angling; *Salvelinus confluentus*; bull trout

INTRODUCTION

Many populations are exploited by humans (Coltman et al. 2003, Hilborn et al. 2003, Cowlishaw et al. 2005), and in some cases are severely overharvested (Pauly et al. 2002, Post et al. 2002, Hilborn et al. 2003, Allan et al. 2005). The ability to compensate for harvest-induced changes has important implications for the regulation and sustainability of populations. Changes, not only in survival, but in reproductive output through changes in growth, maturation and reproductive effort could be significant (Lorenzen and Enberg 2002, Hutchings 2005). Therefore, understanding how these traits respond to exploitation affects our ability to predict and manage populations (Conover and Munch 2002, Olsen et al. 2004, Hutchings 2004).

Density-dependent growth has been demonstrated in a number of systems (Jenkins et al. 1999, Post et al. 1999, Lorenzen and Enberg 2002). Harvest related declines in density, and therefore competition, may encourage higher individual growth rates (Engelhard and Heino 2004b, Reznick and Ghalambor 2005). However, life history theory predicts that organisms must balance the trade-offs between energy allocation to somatic growth, reproduction and somatic maintenance to maximize their fitness (Roff 1992 , Stearns 1992, Gurney and Middleton 1996, Bertschy and Fox 1999). Therefore, any changes in growth or survival may alter life history characteristics such as fecundity, age and size at maturation, and spawning frequency (Stearns and Koella 1986, Bertschy and Fox 1999, Magnan et al. 2005, Jørgensen et al. 2006). The evolution of phenotypic plasticity in life history traits may in itself be an adaptive response to variable environmental conditions (Levins 1963, Houston and McNamara 1992, Scheiner 1993). The ability for a life history characteristic to change and the rate at which it changes depends upon both its genetic basis and its phenotypic plasticity (Shuter and Abrams 2005). Although growth and age- and size-at-maturation are relatively plastic traits (Rochet 1998, Bertschy and Fox 1999), harvest mortality, which is often size-selective, has also been shown to have evolutionary consequences if the trait is heritable and there is a strong enough selection differential (Law 2000), (for example, Conover and Munch 2002, Coltman et al. 2003, Olsen et al. 2004). These harvest-induced evolutionary changes in life history characteristics can occur at rates much faster than originally thought and over periods relevant to resource managers (Conover and Munch 2002, Reznick and Ghalambor 2005, Carroll et al. 2007), but the period required to reverse these changes may be long (Hutchings and Reynolds 2004, Hutchings 2005, de Roos et al. 2006, Walsh et al. 2006) and furthermore may limit population recovery (Hutchings 2000, Law 2000, Conover and Munch 2002, Walsh et al. 2006). Therefore the degree to which life history traits can compensate for exploitation through increased productivity, the impact of depensatory processes and harvest-induced evolution, and the time scales at which these processes occur are important for predicting a population’s response to changes in harvest rates. Understanding these processes regulating population dynamics will allow for more effective management (Trippel 1995, Rochet 2000, Lorenzen and Enberg 2002).

The intent of this study was to examine the life history response of an overexploited iteroparous salmonid population, bull trout (*Salvelinus confluentus*), to the elimination of harvest mortality. Bull trout live in relatively cold, unproductive mountainous streams, rivers and lakes of north-western North America, and are late maturing and slow growing in relation to most other salmonids, making them particularly susceptible to overexploitation (Post and Johnston 2002, Post et al. 2003). Due to their decline in abundance and distribution in the last century, bull trout are currently listed as “sensitive” in Alberta, Canada (Alberta Sustainable Resource Development 2001) and as “threatened” under the Endangered Species Act in the coterminous United States (U.S. Fish and Wildlife Service 1999). The bull trout population in Lower Kananaskis Lake, Alberta, Canada, is no exception and was in decline from 1947 until 1992, primarily due to overfishing (Stelfox 1997). This species is highly vulnerable to angling due to its opportunistic feeding behavior, and because individuals attain a catchable size several years prior to maturation (Post and Johnston 2002, Paul et al. 2003). By 1992, the spawning population was depressed to 60 spawning adults, at which time fishing regulations were changed to catch-and-release (Johnston et al. 2007).

The bull trout population in Lower Kananaskis Lake provides a rare opportunity to examine the changes in life history characteristics over a wide range in density as it rebuilt after overexploitation. This population experienced a 28-fold increase and approached an adult carrying capacity within a ten year period after catch-and-release regulations were implemented (Johnston et al. 2007). A demographic analysis clearly demonstrated that density-dependent survival of both adults and juveniles limited population growth in this system (Johnston et al. 2007). Due to the large changes in density, it is hypothesized that growth rates in addition to survival rates may have changed in this system and that phenotypically plastic life history characteristics, such as age- and size-at-maturation, and reproductive frequency, that are linked to changes in growth and survival may have resulted. Therefore, the objective of this study was to determine if there was evidence of density-dependent growth, maturation, and reproduction.

While density-dependence is a well studied ecological process, this system provides the unique opportunity to: 1) monitor a population through the entire recovery process and examine the extent to which the population was able to compensate for overharvest; 2) monitor these changes in a natural system; and finally, 3) monitor the response of individuals of both genders to the changes in density for a variety of life history characteristics. Results from this study have implications for population growth and regulation and the management of this threatened species.

METHODS

Study area

Lower Kananaskis Lake is a 646 ha reservoir located in Peter Lougheed Provincial Park, Alberta, Canada (Johnston et al. 2007). It has only one inlet stream, Smith-Dorrien Creek, that provides suitable spawning habitat for the native bull trout population (Stelfox and Egan 1995). Prior to April 1, 1992, anglers were allowed a daily harvest of two bull trout (5 bull trout prior to 1984) with a minimum size of 40 cm (no size limit prior to 1987). However at 40 cm the majority of fish are not yet sexually mature (Johnston 2005). By 1992, the spawning population had declined to 60 spawning adults (Johnston et al. 2007). In response, zero harvest regulations, a bait ban and an area closure of the spawning habitat were implemented on April 1, 1992.

Life history

The adult bull trout in Lower Kananaskis Lake are generally adfluvial and therefore only leave the reservoir during the spawning season. They commence their spawning migration between August and September and return downstream between September and early November (Mushens 2003, Johnston 2005). Young bull trout hatch the following spring and remain in the creek for one to four years before migrating to the reservoir. The juveniles then spend an additional one to five years as immature fish before reaching maturation at approximately seven years of age (range six to nine). Bull trout are iteroparous; however, individuals may not always spawn in sequential years (Johnston et al. 2007).

Field methods

The abundance of bull trout spawners in Smith-Dorrien Creek was enumerated annually during their spawning migration. A fish fence and bidirectional traps were installed at the mouth of Smith-Dorrien Creek at the beginning of each spawning season. This structure was in place for the majority of the spawning season (early to mid-August until mid- to late October) making it likely that a fish was caught moving in at least one direction of their migration, as they only spend about 30 days on average upstream. This was done for the years 1992 to 2002, excluding 1994 when the fence was not installed. Individuals caught in the trap each year are assumed to represent a complete census of the spawning population (except in 2001 when trapping was incomplete). The upstream trap was not installed in 2001 but was replaced with a unidirectional incline plane. However, in 2001 the entire creek was electrofished prior to the removal of the trap. At this time approximately 6% of the spawning population remained upstream suggesting that most fish had returned to the reservoir by the time the fence was removed and as a result were likely caught in the trap while moving downstream. Details of how we estimated adult population abundance and spawning abundance in 2001 are discussed in Johnston et al. (2007). Electrofishing was used to assess the relative abundance of juveniles in Smith-Dorrien Creek from 1995 to 2003. More detailed field methods are described in Johnston (2005) and Johnston et al. (2007).

A key component of this research was that captured fish were given a unique tag, allowing individuals to be tracked over years. Adults or fish greater than 400 mm were tagged with individually coded Floy® tags and VI Alpha visual implant tags in addition to having their adipose fin removed to identify them as previously captured individuals. Juveniles electrofished in Smith-Dorrien Creek were PIT (Passive Induced Transponder) tagged and given an upper caudal fin clip. Multiple methods of marking individual fish aided in their future identification in the event of tag loss. Captured fish were weighed, fork length was measured, and where possible sex and state of maturity was determined (i.e., green, ripe or spent). Fish were anaesthetized prior to tagging using either clove oil or tricaine methanesulfonate (MS 222). Trapped fish were released above or below the trap in relation to their original direction of travel and after consideration of their reproductive state. Electrofished juveniles were released within the area of their captured. By tracking individuals within and among years, we were able to determine the abundance of adults in the system (described in Johnston et al. 2007) and to examine individual changes in growth and reproductive characteristics as the population rebuilt.

Growth

Changes in mean size-at-age were used to determine if there was evidence of density-dependent somatic growth during the juvenile stage. This is because, unlike for adults, we did not recapture the numbers of individuals required to look at individual growth rates. A linear mixed model was used to describe the relationship between the number of eggs that produced the cohort and size-at-age using Proc Mixed in SAS® (SAS Institute Inc. 2001). Age was included as a categorical variable, and the day of the year on which the sampling took place was also included in the model to account for the growth that occurs during the summer season due to variation in the timing of electrofishing events among years (see Appendix C Table C1 for models examined). Juvenile size was standardized to their fork length on August 15th, an arbitrary date central in the distribution of electrofishing events, for presentation purposes by adding deviations from the predicted mean on the day of capture to the predicted mean on August 15th. A similar analysis was used to determine the effect of egg density on the relationship between juvenile fork length and mass (see Appendix C Table C2 for models examined). An individual's mass-at-length is often assumed to indicate an individual's energetic condition and potentially their fitness (Jones et al. 1999). Repeated measures information that was available (i.e. recaptured PIT-tagged juveniles) was accounted for in both of these analyses.

Density-dependent growth in adults was determined by examining individual growth rates in length and mass and changes in condition (see Johnston et al. 2007 for abundance estimates). However, unlike for juveniles, we were able to examine annual growth increments for both length and mass of adults because we repeatedly captured numerous individuals over the course of the study. Density-dependent growth relationships were examined for individuals that were captured in two consecutive years using a linear mixed model (Proc Mixed) (SAS Institute Inc. 2001). Repeated measures were accounted for to correct for the violation of the assumption of independence due to the multiple captures of individuals (described in Appendix C). Sample sizes were often very large (see Table A1 for a data summary) and as a result the ability to detect statistically significant relationships was high even though these relationships may not have been biologically significant. To address this problem, AICc values (Burnham and Anderson 2001) in addition to parametric statistical tests of significance ($\alpha = 0.05$) were utilized to determine the most parsimonious and statistically best fit model from a series of candidate models that were constructed in the form of a backward stepwise regression that included all candidate variables and interactions (see Appendix C). The most parsimonious model based on AICc values that was statistically significant was chosen as the best fit model (see Appendix C for models examined and AICc values). Sex and initial size were included in the models when examining the effect of population density on individual growth rates, because although fish have indeterminate growth, growth rates decline as they approach an asymptotic size (Haddon 2001). Fabens' linear translation of the asymptotic von Bertalanffy growth curve (Haddon 2001)

$$\Delta L = (L_\infty - L_t)(1 - e^{-K[\Delta t]}) \tag{1}$$

was used to convert model results to standard growth parameters where; ΔL = change in length over the period Δt, L_t = an individual's length at time t, L_∞ = asymptotic maximum body size, K = growth rate parameter, and Δt = change in time from time t to present.

Maturation

Mean size-at-maturation was estimated using the size of fish that spawned for the first time. This assumes that the year that sexually mature fish were captured for the first time represents their first reproductive event and the year that the maturation process was completed. This assumption is likely violated in 1995 and 2002 as no spawning census was taken in 1994 and the census was incomplete in 2001. The years 1991 to 1993 were removed from the analysis because we know little about the reproductive history of these fish and we only had very small sample sizes available. Density-dependent changes in size-at-maturation were determined using a generalized linear model (Proc GLM) (SAS Institute Inc. 2001). Repeated measures were not considered in this analysis, since a fish only matures once.

Age-at-maturation was estimated for a subsample of fish from 1995 until 2002 for which age information was available (i.e., mortalities [natural and culled] or fish PIT tagged as juveniles). Therefore, it is also assumed that the age-at-maturation of these fish was representative of their spawning cohort. The relationship between age-at-maturation and density was analyzed using a cumulative logistic regression with a multinomial distribution (Proc Genmod) (SAS Institute Inc. 2001). This analysis fits the probability of maturation at age-6, at age-6 or -7, and at age-6 to -8 older (see Appendix D). Repeated measures were not a concern in this analysis. Similar to size-at-maturation, fish captured in 1991 to 1993 were not included in the data set due to our lack of knowledge about their reproductive history and the small sample sizes. For simplicity and clarity of presentation, mean age-at-maturation was also examined using the same methods as described above for size-at-maturation. However, due to age being an ordinal rather than continuous variable the cumulative logistic regression is the more rigorous analysis (Appendix D).

Fish age was determined from otolith sections, pectoral fin ray sections, and length-frequency analysis of fish captured as juveniles (see Johnston 2005 for methods). Fish age was estimated by counting seasonal growth rings (annuli) in calcified structures such as sagittal otoliths and pectoral fin rays from incidental mortalities (Graynoth 1996, Haddon 2001). In addition, a body length-frequency analysis was also used to estimate the age of juveniles (see Johnston et al. 2007). To validate the various aging techniques, comparisons were made between the three techniques where samples were available (i.e. fish that were captured as juveniles and at some later stage died). Oxytetracycline (OTC), a compound that binds with the calcium in boney structures to produce a time mark (Hall 1991), also validated the ages by determining that the annuli were deposited yearly.

Fecundity and reproductive effort

The length-fecundity relationship, calculated using 26 ripe female mortalities from 1999, was used to estimate the number of eggs produced in a single season (see Johnston et al. 2007). The mean egg count of three subsamples taken from a female was multiplied by the total egg mass to obtain the total egg abundance produced by an individual female. Linear regression analysis (Proc GLM) (SAS Institute Inc. 2001) was used to obtain the length-fecundity relationship (log-transformed data) reported in Johnston et al. (2007) and a mass-fecundity relationship. The length-fecundity relationship was used to determine population fecundity as length was available for almost all females that spawned, while upstream mass was not. The assumption was made that the length-fecundity relationship does not change with density, which may not be the case if female condition is density-dependent. Any changes in mass-at-length may indicate changes in the length-fecundity relationship. However, the magnitude of the change in estimates of total egg abundance caused by density-dependent individual fecundity are likely to be minor in comparison to the changes caused by the 20 fold increase in female-spawner abundance over the course of the study.

Reproductive frequency

The occurrence of spawning in this system was demonstrated to be irregular, with not all fish spawning in all years (Johnston et al. 2007). To determine if the propensity to skip spawning events was related to density, the effect of adult abundance on the proportion of fish missing reproductive bouts was examined using logistic regression analysis (Proc Genmod)

(SAS Institute Inc. 2001) (Tables C16 and C17). Data from 1995 to 2000 were used for this analysis as population (Table A1) estimates in the 2001 and 2002 had time series biases and because of the incomplete census in 2001. This analysis was completed for all adult fish, and then for first-time spawners only to see if age affected the results.

To examine differences between fish that skipped spawning and those that didn't, a subset of the data was used. Only fish that skipped one year (i.e. spawned, skipped, spawned), or fish that spawned every year for three years in a row were used (i.e., spawned, spawned, spawned) (Figure 1, e.g. year x+1 to year x+3). By only including these fish in the analysis, the data do not represent the total proportion of fish missing reproductive events at any given time. However, this framework does allow us to test for density-dependence without concerns about a time series bias associated with the truncation of the study. We assume that this subsample is representative of the population. The periods from 1995-1997, 1996-1998, 1997-1999, 1998-2000, and 1999-2001 were used (Table A1). 2000-2002 was not used due to the incomplete spawner census in 2001. As a result of this incomplete census, it is likely that the sample size for the 1999-2001 period was reduced. However, the proportions would be the same regardless of sample size assuming fish that repeatedly spawned and those that skipped a year were caught in same proportions in 2001.

Differences in growth and survival between fish that spawned repetitively and those that skipped spawning were investigated to assess the costs and benefits of the two strategies. Biennial growth in the length and mass of individuals was examined to determine if non-repetitive spawners had higher growth rates than fish that spawned repeatedly. We included fish that spawned for three consecutive years versus fish that had spawned, skipped a year and then spawned (Figure 1). Using this same sample, condition of fish prior to and after missing a spawning event was compared with the mass-at-length of fish in the same years that spawned repeatedly over the same time span. Annual growth in fork length prior to the period in which fish may or may not have skipped a reproductive bout, as well as the annual growth after this period was examined for differences between the two strategies (Figure 1). It is assumed for these analyses that fish that were designated as non-repetitive spawners because they were not captured at the trap were unable to spawn in Smith-Dorrien Creek or any other location. For the reasons outlined above, only the periods from 1995-1997, 1996-1998, 1997-1999, 1998-2000, and 1999-2001 were used (Table A1). A mixed linear model accounting for repeated measures (Proc Mixed) was used to assess differences in growth/condition between non-repetitive and repetitive spawners (SAS Institute Inc. 2001) (Appendix C). Included in the model as covariates were sex, fork length and density as these core factors influenced growth and condition. The least-square means (LS means) from these analyses are presented.

Finally, survival of non-repetitive versus repetitive spawners was examined using logistic regression analysis (Proc Genmod) (SAS Institute Inc. 2001). Similar to the data used in the growth/condition analyses above, fish that spawned, did or did not spawn, and then spawned again were examined to see if they survived an additional year (Figure 1). As a result, only fish alive in the 1995-1997 surviving to 1998, fish alive in 1996-1998 surviving to 1999, and fish alive from 1997-1999 surviving to 2000 were used in this analysis due to the incomplete census in 2001 (Table A1). Density was included in this model due to the previous establishment of density-dependent survival of adults in the system (Johnston et al. 2007). This analysis was completed for all adult fish, and then for first-time spawners only, to control for survival differences due to senescence.

Evolution

The influence of natural selection on adult growth was examined using the methods outlined in Carlson et al. (2007). Survival of fish from one spawning season to the next was used as the metric of fitness. Fish that were recaptured after the focal period were assigned an absolute fitness of 1 and those that were not captured again were assigned an absolute fitness of 0. As a result, data for survival from 1995-96 to 1999-00 for all fish and only first-time spawners (Table A1) were used for this analysis as population estimates in the 2001 and 2002 had time series biases and because of the incomplete census in 2001. The opportunity for selection (*I*), the variance in relative fitness (Brodie et al. 1995), which represents the upper limit for the strength of selection, was calculated on an annual basis. Relative fitness was an individual's absolute fitness divided by the mean absolute fitness in a year (Carlson et al. 2007). We also estimated the strength and form of selection. As outlined in Carlson et al. (2007), we used logistic regressions (Proc Genmod) (SAS Institute Inc. 2001) to determine the effects of body length on absolute fitness on linear and non-linear selection differentials. Absolute fitness was regressed against standardized body length (which was calculated as the deviation of an individual's length from the mean length of the adult population in that year and divided by the standard deviation) to determine the total strength and direction of selection on fish length. In a second logistic regression, absolute fitness was regressed against standardized length and standardized length squared. The coefficients of this relationship describe if selection is disruptive or stabilizing (Carlson et al. 2007). It should be noted; however, that because these analyses rely on body size it is not a complete census of the population in the year. Fish that skipped spawning were not included in the analysis in the year that they did not spawn as their size was unknown. Due to the insufficient data on individual juveniles and their survival to maturity and the lack of aging data, we were unable to examine other evolutionary changes in life-history characteristics such as survival to maturity and the timing of maturation.

RESULTS

Growth

There was no evidence of density-dependent growth of juvenile bull trout during their residence in the creek. Egg density had no significant effect on the standardized mean size of juveniles within an age class ($F_{1,566} = 0.01$, $P = 0.9193$, $n = 594$, Table C1) (Figure 2a), although mean size between age classes did vary (Table B1). The standard deviation (SD) and the coefficient of variation (CV) around mean fork length for each age class in each year also did not show any density-dependent trends (Table B1). Density was not part of the most parsimonious model to describe mass-at-length (see Appendix C Table C2) (Figure 2b).

In contrast, there was strong evidence that density significantly influenced growth in body size of adult bull trout in Lower Kananaskis Lake (Figure 3) (see Table C3 & C7 for model selection). Individual annual growth in fork length was inversely related to adult abundance and fish length (Figure 3 a & d) (Table B1). In addition, the body size at which growth rates approach zero is smaller in high density environments, a reflection of changes in asymptotic size. This observation was more pronounced in females than males due their lower overall growth rates. Annual growth in upstream mass was also density-dependent and inversely related to fish size (Figure 3 b & e) (Table B1). A residual analysis demonstrated no relationship with length and a normal distribution ($F_{1,\,1002} = 2.96$, $P = 0.0854$, $n = 2138$, also see Appendix E Figure E1), suggesting that the relationship between length and growth in mass approached a linear one for fish of large size (i.e., above the inflection point in the sigmoid curve). In addition, it was more common for larger fish to experience negative growth in mass at high density, with males experiencing a faster decline in growth in mass than females (as is demonstrated by the steeper slope of the growth increment – fork length relationship in Figure 3, Table B1).

A decrease in growth in mass does not necessarily imply that a fish at a given length is lighter. A fish with a lower growth in mass may also have a corresponding decrease in growth in length, resulting in a similar mass-at-length (see Table C11 for model selection). A density-dependent change in mass-at-length was detected in this study (Figure 3 c & f) (Table B1), although it did not result in large changes in fish condition. However, this type of allometric relationship is often very tight (e.g. juvenile condition) and density did explain some of the remaining variance. Increases in density resulted in fish being lighter at a given length and the negative effects of density on mass-at-length increased with fish size.

The changes in growth rates and mass-at-length were used to calculate the parameters that are used in standard fisheries growth models. Density-dependent growth resulted in density-dependent decline in the asymptotic size (L_∞) that a fish could attain (Table 1). The asymptotic size (L_∞) was also gender-dependent being lower for females. No estimate of age-at-zero-size (t_0) could be obtained due to the calculation used (see equation 1). Parameters for the length-mass regression were also found to be density-dependent (Table 1). The allometric growth parameter (b) was negatively related to density, whereas the scaling parameter increased exponentially with density.

Maturation

Density influenced both size-at-maturation and the timing of maturation. Mean size-at-maturation changed with density; although density affected the two genders differently (Figure 4) (Table B2) (see Table C18 for model selection). Males increased in size at maturation as the abundance of adults increased. However, the mean size of females at maturation declined with density. Size-at-maturation increased by approximately 19 mm for males, and declined by approximately 11 mm for females when the population experienced an increase of 1500 individuals. This represents over a full year's growth (-1.08 years) for males at high densities and greater than half the annual growth of females (+0.71 years).

Age-at-maturation was also density-dependent. Mean age-at-maturation increased with density for both sexes; however, males delayed maturation longer than females (Figure 4) (Table B2) (Appendix C Table C19). A multinomial logistic regression provided a more rigorous assessment of the timing of maturation (Appendix D Table D1). For both genders, the proportion of fish maturing in an earlier age class (age-6) declined with density (Table B2). These results suggest that the proportion of females maturing at age-6 declined, while the proportion of females maturing at age-7 or greater than age-7 increased with density (Figure 4). Males generally matured later than females, with similar proportions maturing at age-6 or age-7 at low densities. As density increased, the proportion of males maturing at age-6 declined rapidly, while the proportion maturing at age-7 increased slightly. At high densities the number of males maturing at age-6 was low, the number maturing at age-7 also began to decline, and an increase in the number maturing at age-8 was observed (Figure 4).

Fecundity and reproductive effort

Female fecundity was positively related to fork length (FL in mm) (Johnston et al. 2007) and mass (W in g) (Table B3).

(2) $E = 1.72 \times 10^{-3} * (FL^{2.31})$ ($r^2 = 0.78$, $P < 0.0001$, $n = 26$) (Johnston et al. 2007)

(3) $E = -254.65 + 2.08 * W$ ($r^2 = 0.80$, $P < 0.0001$, $n = 26$)

The number of eggs produced per unit body size may also be density-dependent. Unfortunately, since fecund mortalities only came from a single year, we were unable to test for density-dependent changes in these size-fecundity relationships. Regardless, given the occurrence of density-dependent growth and condition, the lifetime fecundity of individual females likely declined considering that survival of adults was also found to be density-dependent (Johnston et al. 2007).

We explored the biological significance of density-dependent growth by examining how much an individual's fecundity and mass differed after one year of growth in a low or high density environment (Table 2). Model predictions suggests that a small female (550 mm) growing in a low density environment (60 adults) is predicted to be 19.7% more fecund at low density than females living in a population at carrying capacity (Table 2). Males of a similar size experience a 16.6% loss in mass which likely affects the amount of mass available for reproductive expenditures. Larger fish (650 mm) were more negatively affected at high density, having negative growth rates in both length and mass (Table 2). For example, it would take a male growing in a high density situation an extra 2.5 years to achieve that same size it took a similar sized male one year to achieve in a low density situation. Compensatory growth also resulted in large females (650 mm) being 28.9% more fecund at low density and large males (650 mm) having a 26.4% increase in mass available for reproductive investment (Table 2).

Therefore, despite having higher growth rates, males were found to be similarly affected by density as females.

Reproductive frequency

The proportion of fish skipping reproductive opportunities was density-dependent. Significantly more fish of both sexes were found to skip spawning opportunities as density increased, but the increase was more rapid for males than females (Figure 5) (see Appendix C Table C16 for model selection, and Appendix B Table B5 for the statistical results). Analysis of the proportion of first-time spawners adopting non-repetitive spawning had similar density-dependent results, suggesting that the increasing trend was not simply a function of an aging population (see Appendix C Table C17 for model selection, and Appendix B Table B5 for statistical results).

The benefits of a skipped spawning strategy were assessed by contrasting the growth rates and condition of fish that were caught at the beginning and end of a three year period (see Appendix C Table C4, C8, C12 & C13 for model selection, and Appendix B Table B4 for the statistical results). Fish that spawned repetitively versus fish that spawned, skipped spawning, and then spawned again (Figure 1) had significantly different condition and biennial growth in both fork length and upstream mass, although this response sometimes varied between the sexes (Figure 6). In the year prior to a potentially skipped spawning opportunity, fish of both genders that skipped spawning were significantly lighter in the year prior than fish that repeatedly spawned (Figure 6a) (females, $F_{1,\,1298} = 141.40$, $P < 0.0001$, $n = 1368$; males $F_{1,\,496} = 24.97$, $P < 0.0001$, $n = 516$). Females that skipped spawning had significantly higher biennial growth rates in fork length than did repetitive spawners (Figure 6c) ($F_{1,\,1546} = 68.36$, $P < 0.0001$, $n = 1551$).

For males no significant difference was found for growth rates in fork length between the two strategies ($F_{1,\,590} = 0.07$, $P = 0.7858$, n =667). However, both females and males that skipped the intermediate spawning event experienced significantly higher growth in upstream mass than repetitive spawners of the same gender (Figure 6d) (females, $F_{1,\,938} = 101.79$, $P < 0.0001$, n =1074; males $F_{1,\,406} = 13.63$, $P = 0.0003$, n =413). When mass-at-length was examined again after non-repetitive spawners skipped spawning, it was determined that both genders returned to spawn at a heavier mass-at-length than those that had spawned repeatedly (Figure 6b) (females, $F_{1,\,794} = 136.80$, $P < 0.0001$, n =1368; males $F_{1,\,374} = 29.61$, $P < 0.0001$, $n = 516$).

To further examine the quality of individuals using the two spawning strategies and the benefits of non-repetitive spawning, growth rates one year prior to and one year after the period when fish potentially did not spawn were examined (see Appendix C Table C5, C6, C9 & C10 for model selection, and Appendix B Table B4 for statistical results). Females that repetitively spawned had significantly higher annual growth rates in fork length (Figure 7a) ($F_{1,\,1086} = 67.65$, $P < 0.0001$, $n = 1308$) and in upstream mass (Figure 7c) ($F_{1,\,711} = 69.07$, $P < 0.0001$, $n = 1056$) than non-repetitive spawners prior to the missed reproductive event. Males showed no significant difference in annual growth in fork length based on spawning strategy, (Figure 7a) ($F_{1,\,373} = 3.18$, $P = 0.0753$, n =415), a similar result to their growth during the missed spawning event. However, males that skipped spawning had significantly lower growth rates in upstream mass prior to skipping a spawning event than repetitively spawning males (Figure 7c) ($F_{1,\,311} = 20.40$, $P < 0.0001$, $n = 344$). Growth rate comparisons differed after fish skipped a reproductive bout. Females that skipped spawning had similar growth rates in length to females that repetitively spawned (Figure 7b) ($F_{1,\,844} = 1.35$, $P = 0.2455$, n =1110), but had significantly lower growth rates in upstream mass (Figure 7d) ($F_{1,\,787} = 6.94$, $P = 0.0086$, $n = 958$). A result similar to before they took a year off. However, the difference between spawning strategies is not as great after the potentially missed spawning event. On the other hand, males that missed spawning the year prior had lower annual growth rates in fork length than males that had spawned repeatedly (Figure 7b) ($F_{1,\,196} = 5.15$, $P = 0.0243$, $n = 210$) but did not have significantly different growth in mass (Figure 7d) ($F_{1,\,167} = 2.41$, $P = 0.1222$, $n = 183$). However, there was still a trend for non-repetitive spawners to have lower growth in mass even after a missed event.

The annual survival of non-repetitive and repetitive spawners in the year following the period in which skipped reproduction might have occurred (Figure 1) was found to differ between the two strategies (Figure 8). Non-repetitive spawners had significantly lower survival than repetitive spawners (see Appendix C Table C14 for model selection, and Table B5). Due to the density-dependent survival of adults in the system (Johnston et al. 2007), the difference in survival between non-repetitive and repeat spawners could vary between less than 10% to greater than 20% depending on the prevailing density. Similar results were observed when survival of first-time spawners was examined (see Appendix C Table C15 for model selection and Table B5), although the difference in survival was less (Figure 8) varying between less than 5% at low densities and near 15% at high densities. This suggests that survival differences are not simply due to senescence. Gender-specific differences in survival rates, with females having higher survival than males generally, were also found (Figure 8).

Evolution

The opportunity for selection (I) was low (All Fish 0.22 ± 0.13 stdev, range 0.11 to 0.45; First-Time Spawners 0.23 ± 0.21 stdev, range 0.08 to 0.55) likely because of the relatively high annual survival rate in the earlier years of the study (All Fish 0.83 ± 0.1 stdev, range 0.69 to 0.90; First-Time Spawners 0.83 ± 0.13 stdev, range 0.64 to 0.93) (Appendix F, Table F1). This suggests that the influence of natural selection on the observed trends is likely small. When all fish were examined directional selection differentials from all years were found to be significant and negative (All Fish -0.50 ± 0.22 stdev, range -0.74 to -0.22) suggesting small fish are favoured (Appendix F, Table F1). First-time spawners had two insignificant linear coefficients (First-Time Spawners -0.39 ± 0.26 stdev, range -0.69 to 0.01). Results from the non-linear quadratic model were only significant in two years for all fish (-0.13 and -0.18), and one year for first-time spawners (-0.31) but these results were negative suggesting stabilizing selection (Appendix F, Table F1).

Summary

The magnitude of the variation of all of the examined life history traits are illustrated in Figure 9, using model predictions. Both survival (i.e., natural mortality) and growth characteristics at low density generally demonstrated a strongly positive compensatory response in relation to these rates at carrying capacity. This was especially true for early juvenile survival (>15 times larger). While juvenile survival after age-1 did not change, survival of adults, especially survival of first-time spawners, varied substantially. Similarly, juvenile growth did not vary, but adult growth did. Even though annual growth translated into a much less dramatic change in asymptotic size, individual growth rates were often >100% greater at low density. While individual fecundity may have been as much as 29% higher at low densities, the number of females spawning resulted in the overall population-level fecundity to be reduced by 95% at low density. The two sexes had different responses to the ecological conditions they experienced. However, although these changes were small in relation to their total body size, they are significant biologically, as they represent differences in almost one year's growth for females and more than a year's growth for males. This translates into gender specific differences in timing of maturation although, generally, the proportion of fish maturing at later ages was reduced at low density for both sexes. The proportion of fish skipping spawning was approximately 85% lower at low density.

DISCUSSION

We observed density-dependent changes in age-dependent survivorship of bull trout in Lower Kananaskis Lake, a population which increased 28-fold after the implementation of zero-harvest regulations and approached an apparent carrying capacity for the adult population (Johnston et al. 2007). Density-dependent changes in survival rates and individual growth characteristics have been reported in a number of systems (Stearns and Koella 1986, Sinclair 1989, Lorenzen 1996 and references therein, Parkinson et al. 2004). Results from this study demonstrate substantial variation in life history traits which can compensate for harvest (Figure 9), which has important consequences to population regulation and sustainable harvest of the fishery (Lorenzen and Enberg 2002, Hutchings 2005).

Growth

Results from Johnston et al. (2007) demonstrate strong differences in natural mortality among life stages, with survival rates being strongly density-dependent prior to age-1 (20 fold difference) (Figure 9). This resulted in little change in the abundance of these younger age classes despite the substantial increase in population-level fecundity (Johnston et al. 2007). Therefore, it is not surprising that growth of juvenile bull trout in Smith-Dorrien Creek was not density-dependent (Johnston et al. 2007). This is consistent with results found by Elliott (1994) that strong density-dependent survival occurs at a critical stage shortly after emergence. However, we did not find a decrease in size variation with density which Elliott (1990a) suggested demonstrates increased competition for territories within a stream. Larger fish, which establish larger territories, are thought to exhaust themselves fighting more adversaries at high densities, while smaller fish are unable to establish territories at all thus removing both ends of the size spectrum (Elliott 1990b, Elliott 1994). However, variation may also be predicted to increase with density if individuals are able to successfully defend and benefit from large or high quality territories. Our results suggest that there was no alteration in the size structure of the population from density-dependent territoriality at these early stages. However, territoriality has been observed in this system (Mushens 2003) and since this critical period would have taken place prior to our sampling, it is possible that any differences in size structure that may have occurred would have been masked by subsequent growth.

In contrast, growth was strongly density-dependent in the older bull trout life stages, likely due to increased competition for limiting resources such as food (Post et al. 1999, Jenkins et al. 1999). In this highly competitive environment, the reduced fitness from density-dependent growth and thus reproduction may change the balance in the tradeoffs between growth, survival and reproduction. Theory predicts the allocation of energy to future reproductive possibilities should cease when the costs associated with maintenance exceed the benefits attained by that allocation (Cichoñ and Kozlowski 2000). Therefore, large females should spawn despite low energetic reserves due to the high fecundity associated with their body size (Jørgensen et al. 2006). The negative growth in mass of the larger fish in Lower Kananaskis Lake suggests that this point was approached or exceeded at high densities. If this was indeed the case, a reduced lifespan of adult bull trout is predicted in this system, and may be one of the mechanisms behind the density-dependent survival observed in this population (Johnston et al. 2007). Furthermore this suggests that in the later years of the study, the individuals that grew up in a lower density situation have outgrown the current prey abundance. Therefore they have low or negative growth as the dynamics of cohort abundance and prey production play out towards a longer-term equilibrium. This energetic dynamic is equivalent to the development of stable age distributions in cohort models after a perturbation and could be responsible for the negative selection differentials that we observed in our examination of natural selection.

For organisms with indeterminate growth, density-dependent growth has important consequences to an individual's fecundity and therefore fitness (Stearns 1992). This study suggests that density-dependence resulted in large declines in individual female fitness (Figure 9). However, the gain in female spawner abundance (i.e., 20-fold over the study period, Johnston et al. 2007) was much greater than the loss from the density-dependent fecundity of individual females, and allowed population-level fecundity to increase dramatically. Therefore, although we see some compensation in these life history characteristics, it is unlikely that reduced fecundity was responsible for regulating this bull trout population. However, density-dependent changes in growth will affect the average size of fish in the system, and may alter the effectiveness of harvest regulations that are size-dependent, making younger fish more vulnerable in heavily exploited systems.

Maturation

The timing of maturation represents the compromise between the benefits and costs of growth and survival and reproduction (Roff 1992, Magnan et al. 2005). However, there are different schools of thought on the impact of decreased growth rates on the timing of first reproduction. If the growth rates decline, it may be better to delay maturation and put all of the energy available into growth as it is assumed that larger individuals produce more and higher quality offspring (Stearns 1992, Hutchings 1993, Fox 1994, Rochet 2000). However, if the benefits of delaying maturation are small, this may not be advantageous (Bell 1980), particularly if mortality rates are high (Hutchings 1996, Haugen 2000, Cichoñ and Kozlowski 2000). In Lower Kananaskis Lake, increased density resulted in delayed maturation (~1 year change in an 8 year period). Observed age-at-maturation may be a phenotypic response to density or the result of selective pressures from natural or harvest-induced mortality (Rijnsdorp 1993, Law 2000, Grift et al. 2003, Olsen et al. 2004, Engelhard and Heino 2004a). As there are no baseline values available prior to exploitation, the artificial selection from angling against late maturing individuals could have occurred when large numbers of juveniles were being harvested, and may have caused some evolutionary response in maturation. The rapid change in age-at-maturation, given the long generation time and the low opportunity for selection (I), supports the hypothesis that this was a compensatory, plastic response rather than an evolutionary response (Rochet 1998, Engelhard and Heino 2004b), although this can not be determined definitively. Importantly, it can not be ruled out that the degree of plasticity observed in this trait was reduced by harvest-induced changes or that natural selection contributed to some of the changes observed. Furthermore the degree of variation in this trait and other life-history traits examined in this study suggests the diversity, that is required for natural and artificial selection to occur, exists if the selective pressures are strong enough and the diversity is in part genetically based.

Size-at-maturation also reflects the trade-offs between growth, survival and reproduction. However, different mechanisms, and their associated trade-offs, can result in the patterns of maturation that we observe (Stearns and Koella 1986). We would expect to see an increase in size-at-maturation in both sexes if a delay in maturation allows an individual to achieve a larger size, and as a result greater reproductive success and offspring survival (Stearns 1992 , Hendry et al. 2001). This is especially true in the case of females where fecundity scales with body size (Stearns and Koella 1986, Jørgensen et al. 2006). However, if the costs associated with delaying maturation exceed the benefits, such as through decreased longevity and lifetime fecundity (Bell 1980, Cichoñ and Kozlowski 2000), it may be beneficial to mature earlier at a similar or smaller size. In Lower Kananaskis Lake, females mature later and smaller, whereas males mature later and larger. The gender-specific response of the Lower Kananaskis Lake bull trout population suggests that these tradeoffs differ among the sexes and an attempt to maintain different traits that maximize that gender's fitness (Crowley 2000, Bedhomme et al. 2003). For example, females may simply need to attain a threshold size before they mature (Day and Rowe 2002); a size at which they are adequately fecund but also a size which they are like achieve given the probability of survival. This threshold may be positively related to the asymptotic size that an individual can attain (Kozlowski 1996, Stamps and Krishnan 1997). Therefore a smaller size-at-maturation is likely in high density environments. The timing of energetic investment in gonadal tissue may also influence maturation, suggesting that females have to commit to a reproductive event earlier than males do (Hendry and Berg 1999, Bunnell and Marschall 2003).

Males, on the other hand, may benefit more from larger size especially in a recovering population where the mean size of the male population is increasing as it ages. Delayed maturation by the larger sex is not uncommon in nature suggesting there is a substantial fitness advantage to achieving a larger size (Bell 1980, Stamps and Krishnan 1997). Male size can be strongly correlated with the success males have in gaining access to and being chosen by a female (Kitano 1996, Fleming et al. 1997, Fleming 1998, Hutchings et al. 1999). The largest males often monopolize the majority of the spawning opportunities, while smaller males that attempt to sneak access to females tend to have reduced success (Kitano et al.1994, Kitano 1996, Fleming et al.1997). The aggressive interactions involved in male-male competition and mate defence may be energetically expensive (Roff 1992, Hendry and Beall 2004) or result in decreased survival (Fleming et al.1997, Hendry and Beall 2004). Density-dependent growth could reduce the perceived quality of males to females and their ability to out compete other males (Wootton 1990, Hendry and Berg 1999). It is the relative size of a male to others that is important. Males maturing at larger sizes will have an advantage over other young males and make them more competitive against larger males experiencing decreased growth in high density environment. Therefore, because the onset of maturation also leads to reduced growth rates due to the allocation of resources to reproduction, it makes sense to delay maturation to achieve a larger size.

Reproductive frequency

After maturation, a portion of the bull trout in Lower Kananaskis Lake adopted a non-repetitive spawning strategy which increased with density. This is a common strategy in a number of species and in a variety of taxa (Bull and Shine 1979, Rideout et al. 2005). Skipped reproduction is generally associated with low productivity and short growing seasons (Bull and Shine 1979, Engelhard and Heino 2006), and is often condition-dependent (Dutil 1986, Jonsson et al. 1997, Alonzo and Warner 2000, Jørgensen et al. 2006) and survival-dependent (Fleming 1998, Jørgensen et al. 2006). Therefore, it is not surprising that the proportion of fish skipping spawning opportunities increased with density. It is assumed that delaying an energetically expensive activity, such as reproductive competition, will result in an increase in either fecundity or survival over the longer term (Bull and Shine 1979, Brown and Weatherhead 2004, Jørgensen et al. 2006). In general, fish growth and condition improved when individuals adopted a non-repetitive spawning strategy, supporting this condition-dependent theory. It has been suggested that skipped reproduction is more common in females (Bull and Shine 1979), which is the gender for which this trait is usually reported due to their obvious contribution to future generations (Rideout et al. 2005). However, Fleming (1998) found that in the subfamily Salmoninae, males were more likely to skip a spawning opportunity than were females, a result that was attributed to lower male survival rates similar to those observed in this system. Since this strategy is often associated with some accessory behavior that is costly energetically, such as spawning migrations (Bull and Shine 1979) or male-male competition and mate defence (Brown and Weatherhead 2004), our results are consistent with the condition-dependent theory. However, the gains achieved by skipped spawning may be short lived. Growth rates the year after returning from a skipped reproductive event tended to be lower than those of repeat spawners, especially for males. As suggested by Brown & Weatherhead (2004), non-repetitive spawners may be poorer quality individuals and, while benefiting from missed spawning opportunities, these individuals may be forever trying to “catch up”. The lower survival rate of spawners that skip reproductive opportunities provides further support for the hypothesis that these are poorer quality individuals which are being selected against, a possible explanation for the negative selection differentials we observed. In combination, the density-dependent declines in individual growth and condition, the increase in the propensity to skip spawning, and the gender specific differences in these traits could have important implications to the overall fecundity of the population and should be considered when making predictions about population dynamics (Purchase et al. 2005). However, in Lower Kananaskis Lake specifically, non-repetitive spawning is unlikely responsible for population regulation because strong density-dependent survival from the egg to age-1 stage (Johnston et al. 2007) would mask any differences in population-level fecundity.

Evolution

The observations of density-dependent growth, condition, maturation and reproductive frequency in the Lower Kananaskis Lake bull trout population suggest the degree to which these life history traits were able to change when the population was heavily exploited by anglers. The rapid response of these life history traits to a substantial alteration of density following restrictive fishing regulations suggests that these traits were phenotypically plastic. However, it is important to consider that some of these changes may also be the result of natural selection. While unlike Carlson et al. (2007) there is little evidence to suggest this was a driving factor during this period, its importance in the long term should not be ruled out. In addition, we can not rule that substantial size-selective harvest may have resulted in evolutionary changes in this system prior to the commencement of the study. Furthermore, the degree of plasticity in these traits may, in itself, be an evolutionarily selected trait. However, on an ecological scale we can say that there is substantial variation in these traits during the recovery of this population (Figure 9). Bull trout in this system appear to be able to compensate to some degree, although not completely, for the overharvest of the population both through growth responses and in reproductive relationships. However, the mechanisms for body-size-dependent reproductive success differ between the genders (i.e., size-fecundity relationships versus non-random mate selection and male-male competition). These sex-specific differences in how life history characteristics respond to changes in density should be recognized as they can influence predictions about sustainable harvest rates (Purchase et al. 2005).

We have demonstrated here and elsewhere (Johnston et al. 2007) that survival, growth, age- and size-at-maturation, and reproductive characteristics are primarily plastic responses over short time scales, and other studies have demonstrated that natural and artificial selection through harvest can result in both plastic and evolutionary changes in these traits (Grift et al. 2003, Carlson et al. 2007, Edeline et al. 2007). Population dynamics are determined by this suite of demographic rates and life history traits. Therefore, these changes have important implications to management as they will determine how populations respond to and recover from exploitation (Hutchings 2000, Lorenzen and Enberg 2002, Goodwin et al. 2006, Jørgensen et al. 2006). However, information about these relationships is often lacking (Goodwin et al. 2006). Our results show that the observed forms of density-dependence in all of the demographic and life-history traits examined lead to population compensation of harvesting mortality. Increased individual growth, earlier maturation, more frequent reproduction and lower mortality at the low densities resulting from harvest all act in a compensatory direction. But it is also clear that prior to the imposition of a catch-and-release regulations that harvest rates were sufficiently high to overcome the compensatory ability of the population.

Management Implications

There are three important management implications of our findings. First, minimum size at harvest regulations, which are common in recreational and commercial fisheries and designed to protect juvenile fish from harvest, may be successful in lightly or moderately exploited populations but not sufficiently restrictive in overexploited low density populations. Therefore models developed to determine sustainable effort and harvest should include density-dependence in these rates and traits or, if this information is unknown, should conservatively use ones determined for low density populations (e.g. Post et al. (2003)). Secondly, we did not find any evidence for Allee or depensatory effects that might hinder population recovery (Hutchings and Reynolds 2004) in the demographic rates or life history traits that we examined. This suggests that this population has a level of resilience to overexploitation. However, we are reluctant to conclude that harvested systems like this one are influenced by processes that are strictly compensatory because there are also a series of harvest related processes that can act in a depensatory manner (Shuter et al. 1998; Post et al. 2002; Post et al. 2008). If these depensatory processes are sufficiently strong, or sufficiently numerous, in harvested populations the net effect can be critical depensation and increasing rates of population decline as populations are exploited (Post et al. 2008). Finally, we have demonstrated substantial inter-individual and population variability in demographic rates and life history traits. This variability allows fish to adapt to adverse conditions (Gurney and Middleton 1996). However, evidence is accumulating that artificial selection from fishing can result in the evolution of genotypes in a direction which may be counter to direction of natural selection (Edeline et al. 2007, Jørgensen et al. 2007, Hutchings and Fraser 2008, Biro and Post 2008). This may make populations maladapted for recovery once harvest is reduced or eliminated in collapsed fisheries (Walsh et al. 2006). It is unknown to what degree, if any, artificial selection by harvest may have caused genetic changes in this population, although it did not appear to inhibit recovery. However, the variability in the traits examined does suggest that there is the strong potential for harvest-induced evolution if these traits are sufficiently heritable. Therefore patterns and processes involved in density-dependent demographic and life history traits are key to our understanding of population, evolutionary and harvest dynamics.

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ONLINE APPENDICES

***Appendix A* – Summary of data used for the analyses**

Table A1

***Appendix B* – Tables of statistical results for final model**

Table B1 – Table B5

***Appendix C* – Repeated measures and model selection methods and results**

Table C1 – Table C19

***Appendix D* – Multinomial logistic age-at-maturation methods and results**

Table D1

Appendix E – Residual plot from analysis of growth in mass

Figure E1

Appendix F – Natural selection analyses results

Table F1

Table 1 Estimates of standard von Bertalanffy growth parameters calculated from model predictions and Fabens' translation, and the allometric parameters of the mass-at-length relationship calculated from model predictions. L_t = an individual's length at time t, L_∞ = asymptotic maximum body size, K = a growth rate parameter, t_0 = hypothetical age when a fish has zero length, W_t = upstream mass of the individual at time t, b = an allometric growth parameter, a = a scaling parameter. Linear regression that accounted for repeated measures was used to determine the most parsimonious model from a series of nested model candidates that described the relationship between growth and the independent variables adult abundance, gender, and size (fork length) and their associated interaction terms. There were 1467 individuals and 2931 observations used in the growth analysis. There were 3263 individuals and 6405 observations used in the condition (mass-at-length) analysis.

Model	**Parameter**	**Estimate**
von Bertalanffy Growth Model	K	0.1904
$L_t = L_\infty \cdot (1-e^{-K*(t-to)})$	Female L_∞	732.6 - 0.0512*Adult Abundance
	Male L_∞	803.3 - 0.0512*Adult Abundance
	t_0	N/A
Length-Mass Regression	Female ln(a)	-9.294 + 0.002099*Adult Abundance
$W_t = aL_t^b$ or	Male ln(a)	-9.227 + 0.002099*Adult Abundance
$\ln(W_t) = \ln(a) + b \cdot \ln(L_t)$	b	2.674 - 0.00034*Adult Abundance

Table 2 The consequences of density-dependent annual growth to the fecundity and reproductive investment of adult bull trout in Lower Kananaskis Lake. Estimated growth in length and mass at low density (60 adults) and at the estimated carrying capacity (1680 adults) (Johnston et al. 2007) based on growth model predictions were compared for small and large fish of both genders. Initial condition was determined from the mass-at-length model predictions. The number of eggs produced was estimated from the mass-fecundity relationship for females. The density difference is the percent deviation at low density, positive or negative (indicated by the sign), from the value at carrying capacity.

		Year 1		**Year 2**			**Annual Growth Rate**	
Density	**Gender**	**Initial Length (mm)**	**Initial Mass (g)**	**Final Length (mm)**	**Final Mass (g)**	**Eggs Produced (#)**	**Length ($mm*y^{-1}$)**	**Mass ($g*y^{-1}$)**
Low (60)	Female	550	1948	581	2228	4383	31.1	280.3
	Male	550	2083	593	2500		43.4	417.1
High (1680)	Female	550	1807	567	1882	3663	16.7	75.3
	Male	550	1932	579	2144		29.0	212.1

Density Difference (%)	Female	-	7.8	2.5	18.4	19.7	86	272
	Male	-	7.8	2.5	16.6		50	97
Low (60)	Female	650	3034	664	3124	6248	13.8	89.6
	Male	650	3245	676	3373		26.0	127.9
High (1680)	Female	650	2567	649	2451	4849	-0.6	-115.5
	Male	650	2746	662	2668		11.7	-77.1
Density Difference (%)	Female	-	18.2	2.2	27.4	28.9	2383	178
	Male	-	18.2	2.2	26.4		123	266

Figure Captions

Figure 1 A depiction of the time periods used for examining differences between fish that skipped reproductive events and those that did not.

Figure 2 Growth of juvenile bull trout electrofished in Smith-Dorrien Creek. Panel (a) describes length-at-age in relation to egg density; and panel (b) the length-mass relationship. Egg density was found to be insignificant in the length-mass relationship (length-mass, P = 0.1213), and not the most parsimonious model in the length-at-age model. Solid lines indicate linear model predictions. Juvenile size was standardized to their fork length on August 15th, an arbitrary date central in the distribution of electrofishing events, for presentation purposes. Repeated measures were accounted for, and 594 observations of 570 individuals were used in this analysis.

Figure 3 Annual growth in length (a & d), mass (b & e), and condition (c & f) in relation to adult density and gender for adult bull trout in Lower Kananaskis Lake. Solid lines indicate linear model predictions. Repeated measures were accounted for in this analysis. n = 2931 observations of 1467 individuals; n = 2138 observations of 1467 individuals; n = 6405 observations of 3263 individuals were used in these analyses for length, mass and condition respectively.

Figure 4 On the left side mean size- (a) and age-at-maturation (b) (mean ± 95 % confidence limits) in relation to total adult abundance and gender for adult bull trout in Lower Kananaskis Lake. Solid lines indicate linear model predictions, n = 3111 and 305 for size and age respectively. On the right side the relationship between age-at-maturation and total adult abundance for bull trout in Lower Kananaskis Lake from the cumulative logistic regression. This is the proportion of fish that spawned for the first time at age-6, age-7, or age-8 or age-9. Lines are the model fit of and symbols are the data.

Figure 5 The proportion of adult bull trout skipping spawning in a given year as a function of gender and adult density in Lower Kananaskis Lake. Lines indicate logistic model predictions; solid for all fish and dashed for first-time spawners (1^{st}). Repeated measures were accounted for in the analysis of all fish. *n* = 6777 observations of 2467 individuals for all fish and *n* = 1604 observations for first-time spawners respectively.

Figure 6 Condition, before (a) and after (b), and biennial growth in length (c) and mass (d) of fish that skip a spawning opportunity in the middle of a 3 year interval compared to those that spawned repeatedly for 3 years by gender. Least Square means from linear models are presented (mean ± 95 % confidence limits) and all other variables were set equal to their mean values for the computation. Models accounted for size and density as covariates, as well as repeated measures.

Figure 7 Annual grow in length (a & b) and mass (c & d), before (a & c) and after (b & d) a potentially skipped spawning opportunity for fish that skipped and those that spawned repeatedly by gender. Least Square means from linear models are presented (mean ± 95 % confidence limits) and all other variables were set equal to their mean values for the computation. The dashed line indicates zero growth. Models accounted for size and density as covariates, as well as repeated measures.

Figure 8 The proportion of adult bull trout surviving after a potentially skipped spawning opportunity for fish that skipped and those that spawned repeatedly as a function of gender and adult density in Lower Kananaskis Lake. Lines indicate logistic model predictions; solid for alternate spawners and dashed for repeat spawners. All fish and only first-time spawners were examined. n = 1136 observations for all fish and n = 643 for first-time spawners respectively. Note that P = 0.0649 for the sex*density interaction term.

Figure 9 Compensatory changes in life history traits. This is a comparison of the predictions of the life history traits examined at low density in relation to carrying capacity. All values represent (x – K)/|K| where K is the value at carrying capacity and x is the value at low density, except for “size-mat time” on the reproduction panel. This is the difference in size at maturity (x – K) divided by the annual growth rate at high density (units = y). Juvenile and adult survival data are from Johnston et al. (2007). FL = Fork Length, sm = small, lg = large, adult k = von Bertalanffy growth constant, L-inf = asymptotic length, mat = maturation, prop = proportion, pop’n = population.

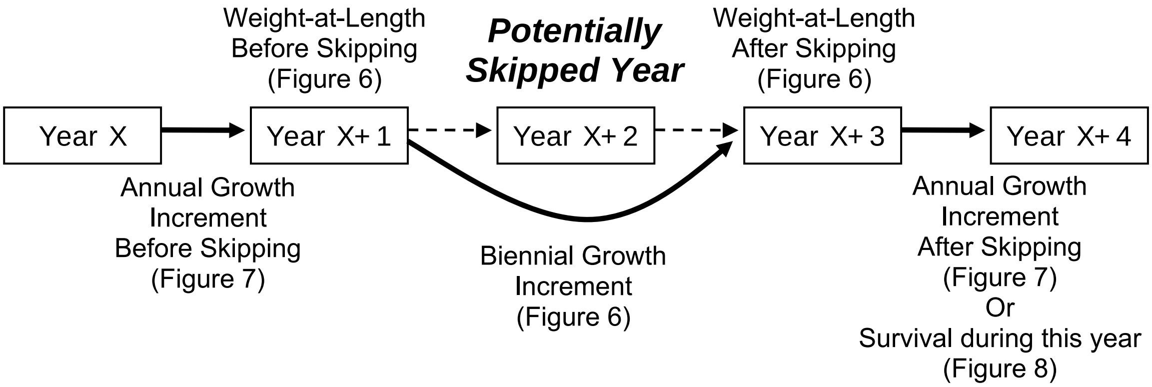
Weight-at-Length
Before Skipping
(Figure 6)
Potentially
Skipped Year
Weight-at-Length
After Skipping
(Figure 6)
Year X
Year X+ 1
Year X+ 2
Year X+ 3
Year X+ 4
Annual Growth
Increment
Before Skipping
(Figure 7)
Biennial Growth
Increment
(Figure 6)
Annual Growth
Increment
After Skipping
(Figure 7)
Or
Survival during this year
(Figure 8)

Figure 1

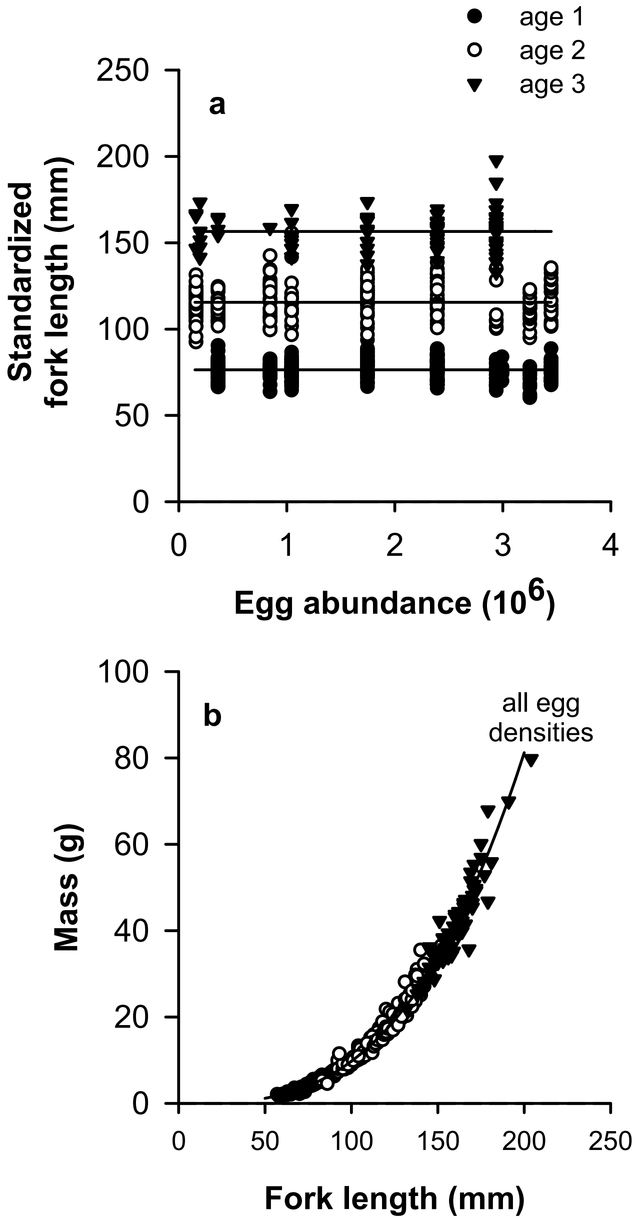
● age 1
○ age 2
▼ age 3
a
Standardized fork length (mm)
250
200
150
100
50
0
0
1
2
3
4
Egg abundance (10^6)
b
all egg densities
Mass (g)
100
80
60
40
20
0
0
50
100
150
200
250
Fork length (mm)

Figure 2

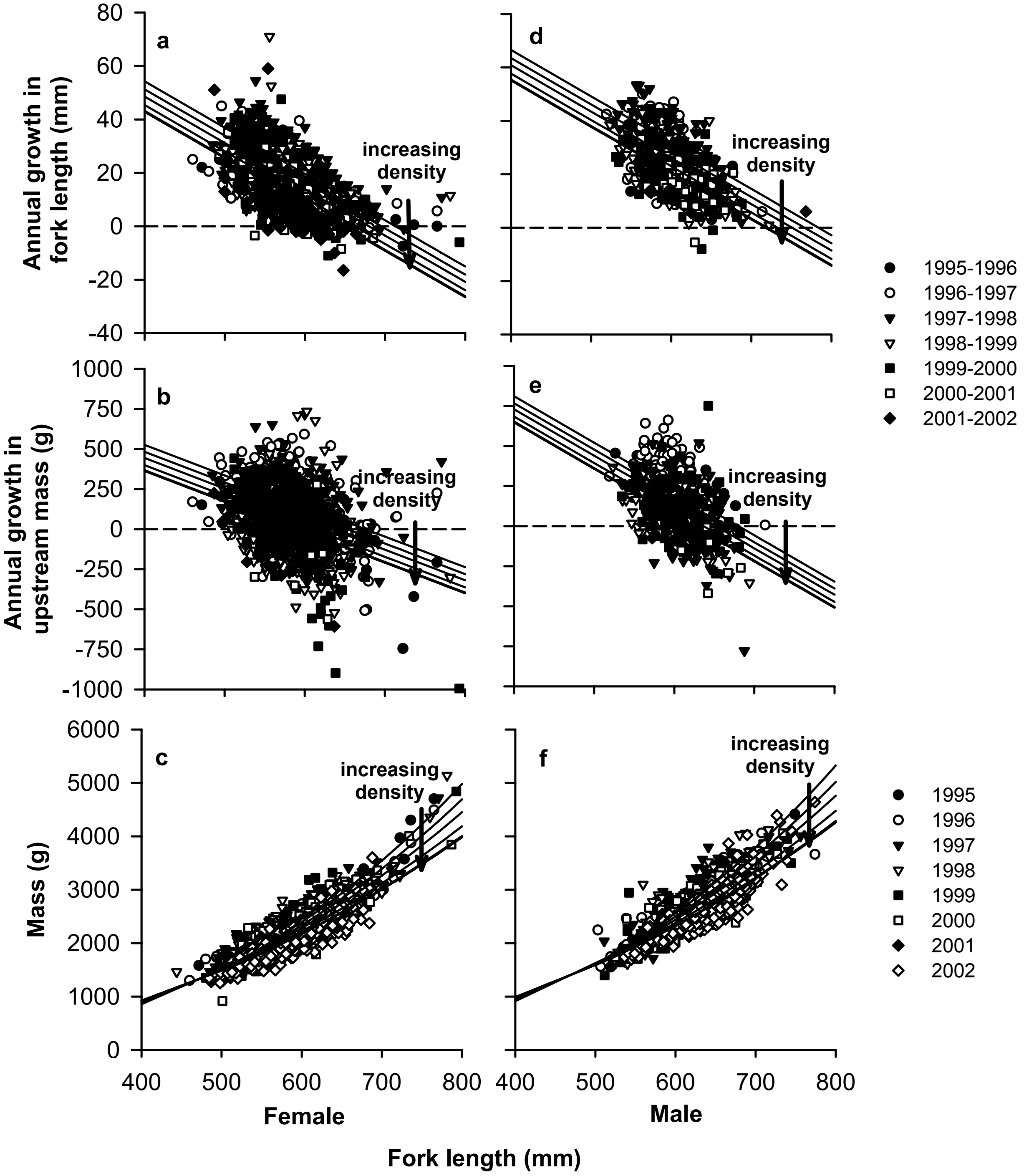
a
b
c
d
e
f
Annual growth in fork length (mm)
Annual growth in upstream mass (g)
Mass (g)
increasing density
Female
Male
Fork length (mm)
● 1995-1996
○ 1996-1997
▼ 1997-1998
▽ 1998-1999
■ 1999-2000
□ 2000-2001
◆ 2001-2002
● 1995
○ 1996
▼ 1997
▽ 1998
■ 1999
□ 2000
◆ 2001
◇ 2002
80
60
40
20
0
-20
-40
1000
750
500
250
0
-250
-500
-750
-1000
6000
5000
4000
3000
2000
1000
0
400
500
600
700
800

Figure 3

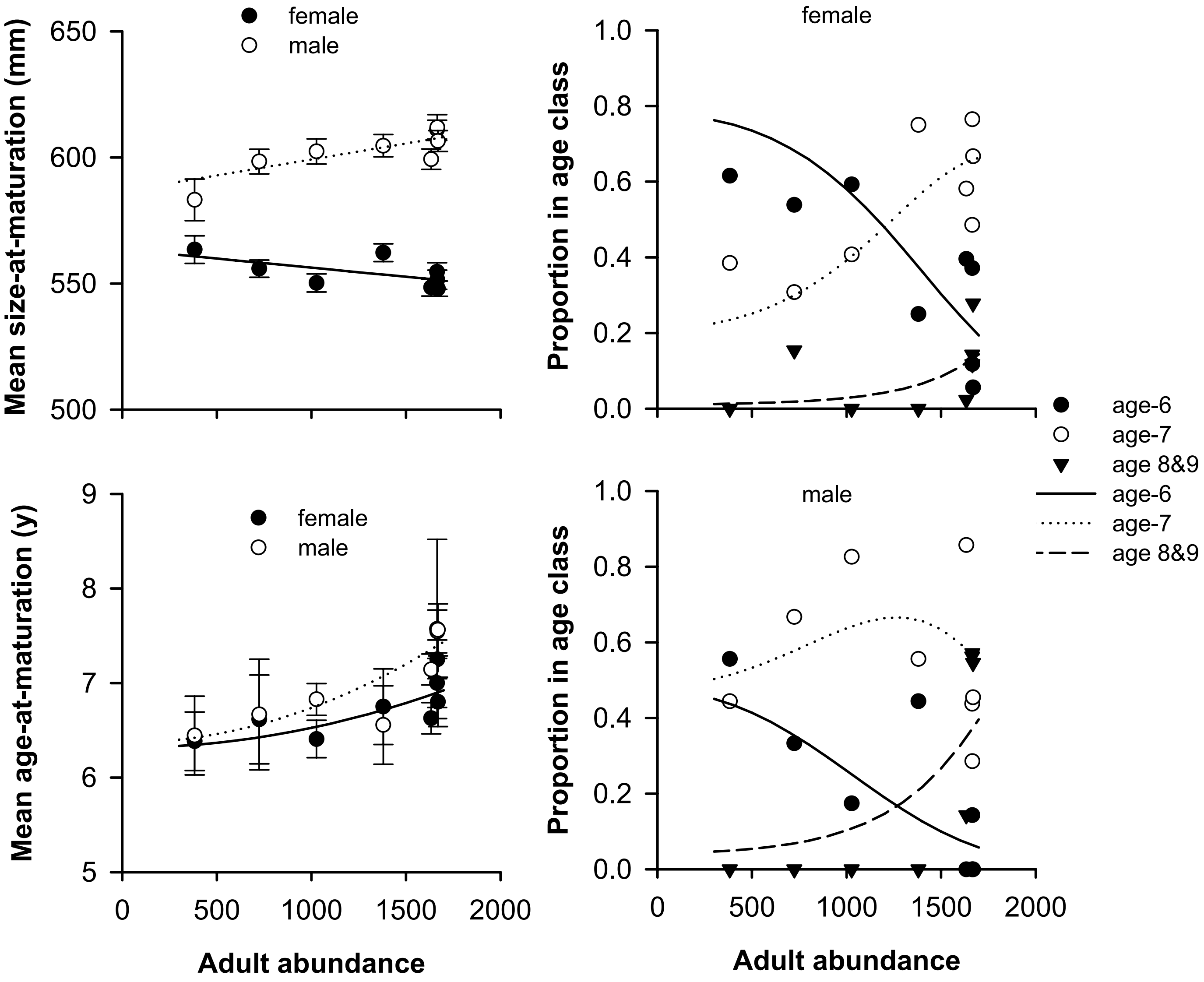
female
male
Mean size-at-maturation (mm)
650
600
550
500
Mean age-at-maturation (y)
9
8
7
6
5
0
500
1000
1500
2000
Adult abundance
female
male
Proportion in age class
1.0
0.8
0.6
0.4
0.2
0.0
age-6
age-7
age 8&9
age-6
age-7
age 8&9

Figure 4

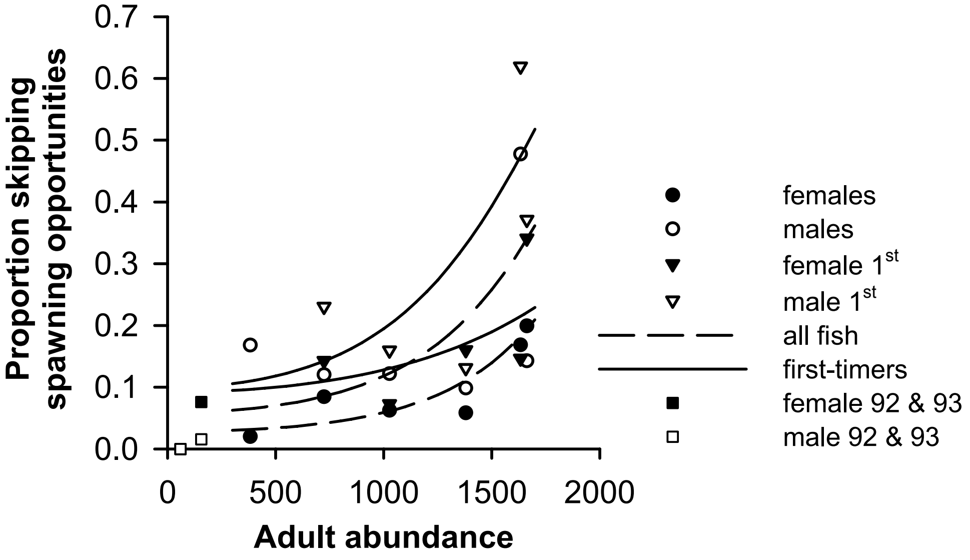
Proportion skipping spawning opportunities
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
500
1000
1500
2000
Adult abundance
females
males
female 1st
male 1st
all fish
first-timers
female 92 & 93
male 92 & 93

Figure 5

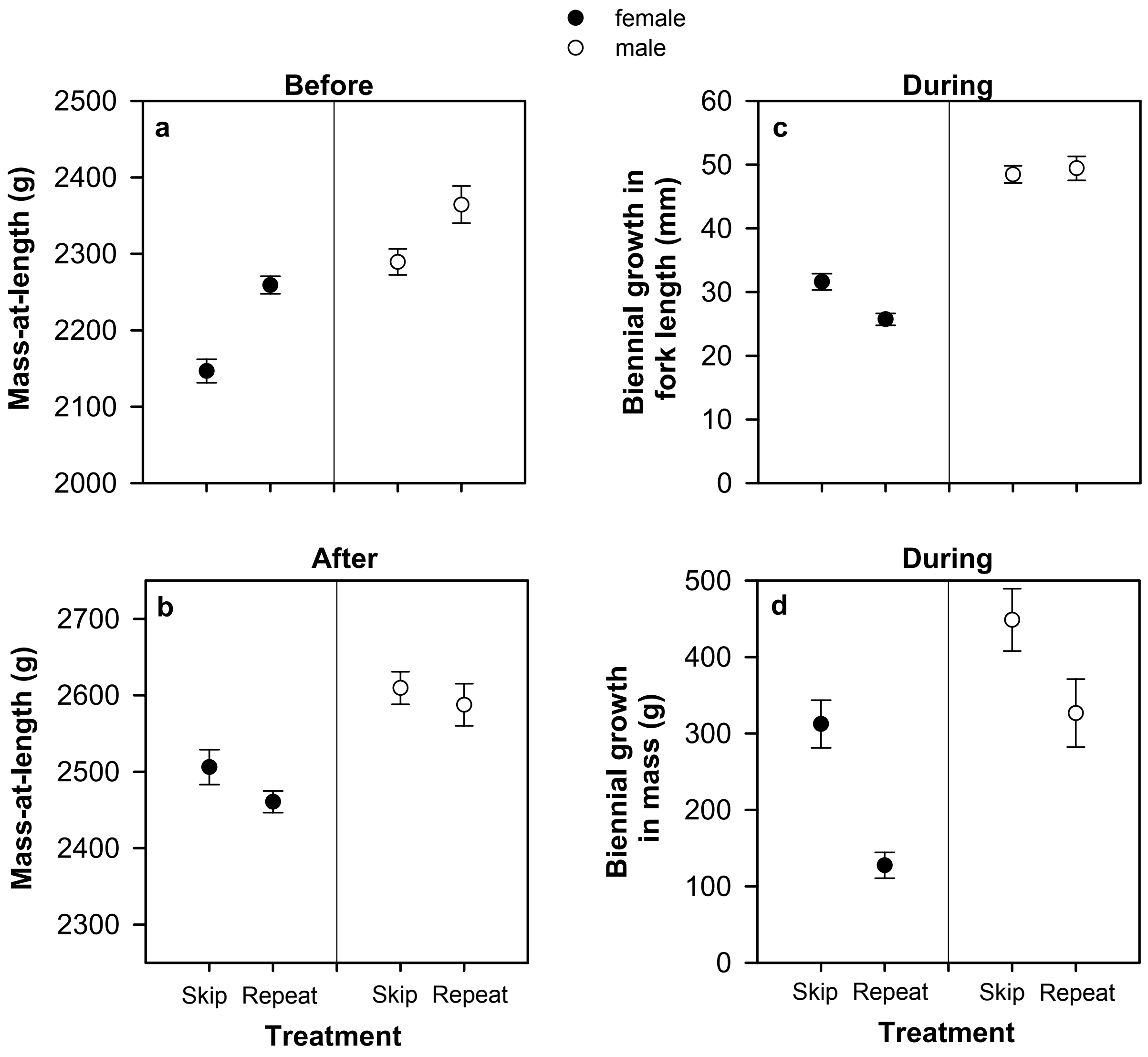
● female
○ male
Before
a
Mass-at-length (g)
2000
2100
2200
2300
2400
2500
After
b
Mass-at-length (g)
2300
2400
2500
2600
2700
Skip
Repeat
Skip
Repeat
Treatment
During
c
Biennial growth in fork length (mm)
0
10
20
30
40
50
60
During
d
Biennial growth in mass (g)
0
100
200
300
400
500
Skip
Repeat
Skip
Repeat
Treatment

Figure 6

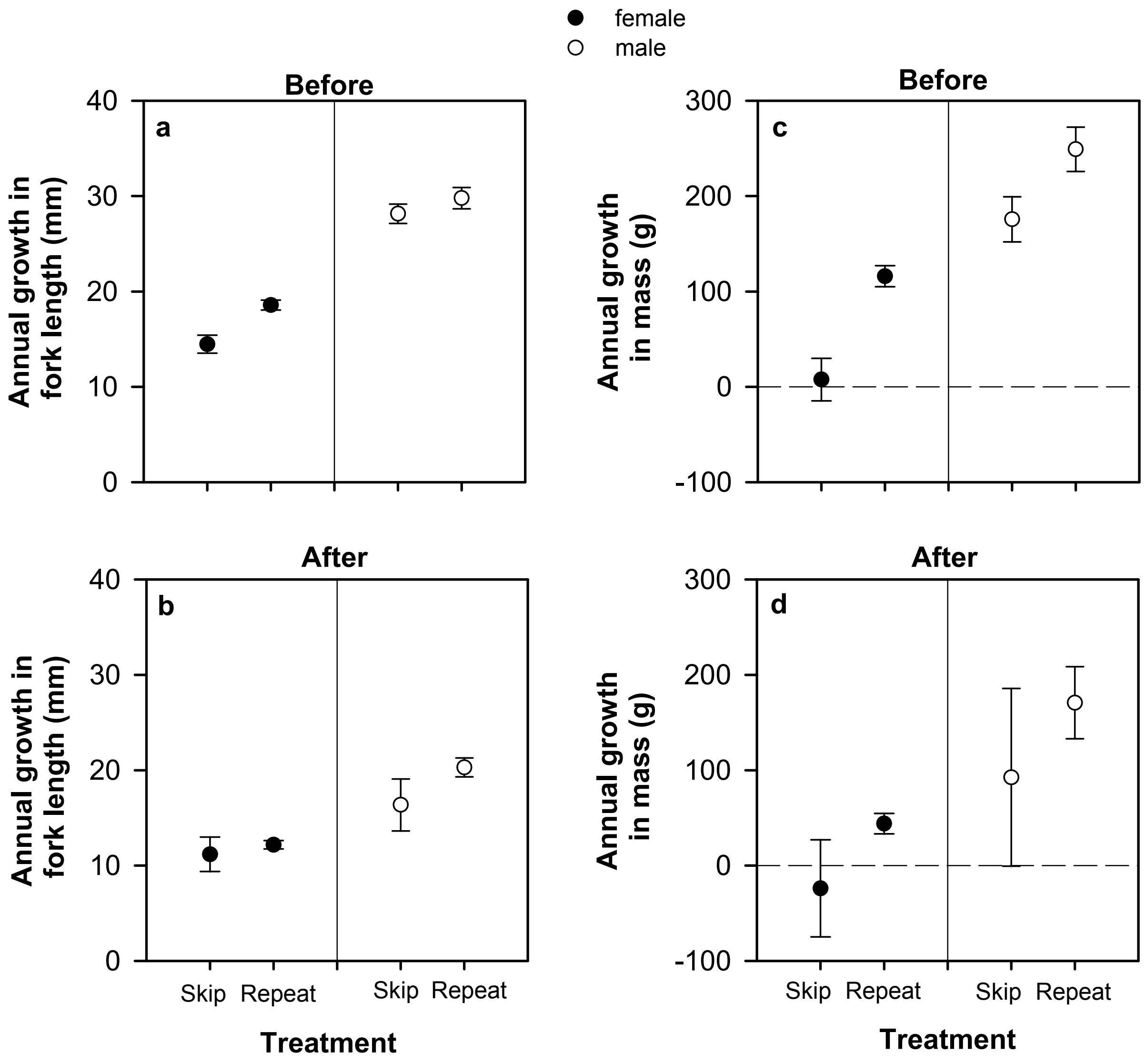
● female
○ male
Before
a
Annual growth in fork length (mm)
40
30
20
10
0
Before
c
Annual growth in mass (g)
300
200
100
0
-100
After
b
Annual growth in fork length (mm)
40
30
20
10
0
Skip
Repeat
Skip
Repeat
Treatment
After
d
Annual growth in mass (g)
300
200
100
0
-100
Skip
Repeat
Skip
Repeat
Treatment

Figure 7

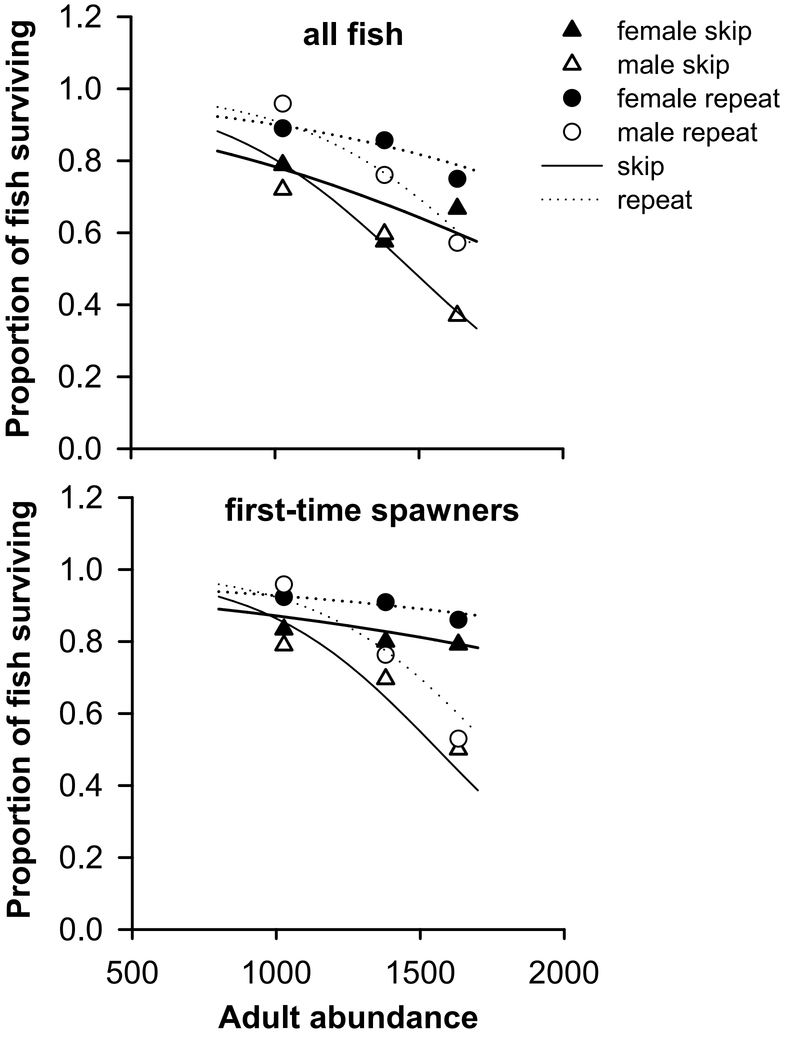
all fish
first-time spawners
Proportion of fish surviving
Adult abundance
1.2
1.0
0.8
0.6
0.4
0.2
0.0
500
1000
1500
2000
▲ female skip
△ male skip
● female repeat
○ male repeat
skip
repeat

Figure 8

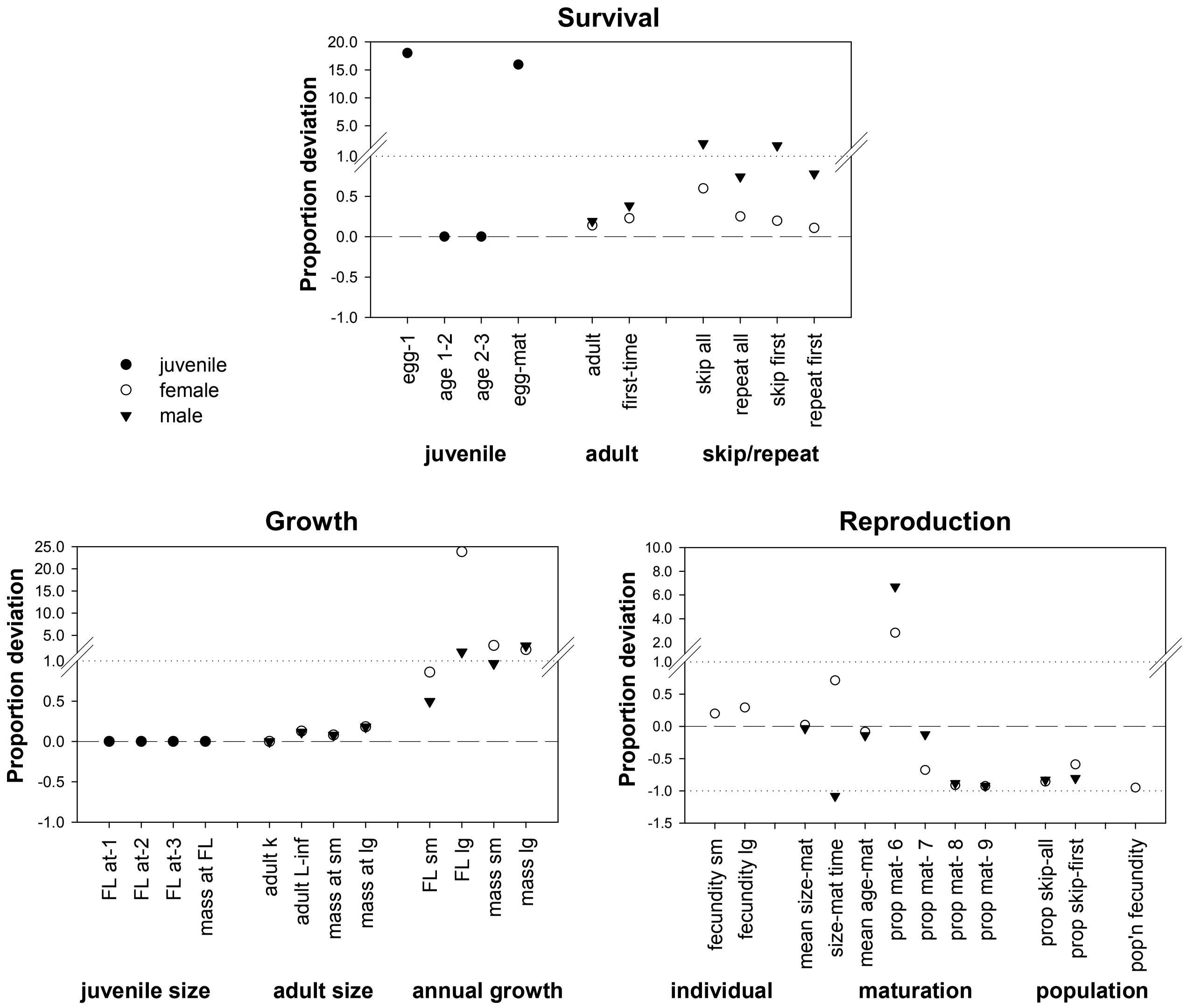
Survival
Proportion deviation
20.0
15.0
10.0
5.0
1.0
0.5
0.0
-0.5
-1.0
egg-1
age 1-2
age 2-3
egg-mat
adult
first-time
skip all
repeat all
skip first
repeat first
juvenile
adult
skip/repeat
● juvenile
○ female
▼ male
Growth
Proportion deviation
25.0
20.0
15.0
10.0
5.0
1.0
0.5
0.0
-0.5
-1.0
FL at-1
FL at-2
FL at-3
mass at FL
adult k
adult L-inf
mass at sm
mass at lg
FL sm
FL lg
mass sm
mass lg
juvenile size
adult size
annual growth
Reproduction
Proportion deviation
10.0
8.0
6.0
4.0
2.0
1.0
0.5
0.0
-0.5
-1.0
-1.5
fecundity sm
fecundity lg
mean size-mat
size-mat time
mean age-mat
prop mat- 6
prop mat- 7
prop mat- 8
prop mat- 9
prop skip-all
prop skip-first
pop'n fecundity
individual
maturation
population

Figure 9