

Density-dependent life-history compensation of an iteroparous salmonid

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Abstract. Over the course of a decade, the bull trout (*Salvelinus confluentus*) population in Lower Kananaskis Lake, Alberta, Canada, recovered from a heavily overexploited state, experiencing a 28-fold increase in adult abundance after the implementation of zero-harvest regulations. This system provided a unique opportunity to monitor the changes in life-history characteristics in a natural population throughout the recovery process. The purpose of this study was to examine the degree to which life-history traits were able to compensate for harvest-induced changes and the implications of this for management. Density-dependent changes in growth, survival, and reproductive life-history characteristics were observed. As density increased, maturation was delayed, and the frequency of skipped reproductive events, primarily by individuals of poor condition, increased. However, size at maturation and the proportion of fish skipping reproduction differed between the sexes, suggesting that life-history trade-offs differ between 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 compensatory 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: angling; bull trout; fecundity; fisheries management; growth; Lower Kananaskis Lake, Alberta, Canada; maturation; phenotypic plasticity; recovery; recreational fishing; *Salvelinus confluentus*; skipped spawning.

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, Hutchings 2004, Olsen et al. 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 pheno-

Manuscript received 12 September 2007; revised 6 May 2008; accepted 3 June 2008; final version received 7 July 2008. Corresponding Editor (ad hoc): J. A. Hutchings.

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typic 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 sufficiently strong 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 density-dependent processes and harvest-induced evolution, and the timescales 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 northwestern 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 zero-harvest catch-and-release regulations (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. The adult population experienced a 28-fold increase and approached an adult carrying capacity within a 10-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 whether 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 1 April 1992, anglers were allowed a daily harvest of two bull trout (five 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 1 April 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 1–4 yr before migrating to the reservoir. The juveniles then spend an additional 1–5 yr as immature fish before reaching maturation at ~7 yr of age (with a range of 6–9 yr). 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 1992–2002, 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 ~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 (Floy Tags, Seattle, Washington, USA) and VI Alpha visual implant tags (Northwest Marine Technology, Shaw Island, Washington, USA) in addition to having their adipose fin removed to identify them as previously captured individuals. Juveniles electrofished in Smith-Dorrien Creek were tagged with a passive induced transponder (PIT) 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 whether 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 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 15 August, 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 15 August. 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 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 Appendix A: 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, corrected Akaike Information Criterion (AIC_c) 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 AIC_c values that was statistically significant was chosen as the best-fit model (see Appendix C for models examined and AIC_c 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),

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

was used to convert model results to standard growth parameters where ΔL is the change in length over the period Δt ; L_t is an individual's length at time t ; L_∞ is the asymptotic maximum body size; K is a growth rate parameter; and Δt is the 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 was likely violated in 1995 and 2002 as no spawning census was taken in 1994 and the census was incomplete in 2001. The years 1991–1993 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 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 2001). This analysis fits the probability of maturation at age 6, at age 6 or age 7, and at ages 6–8 years old (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 (see *Methods: Growth*). 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 for which 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 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 whether 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 2001) (Appendix C: Tables C16 and C17). Data from 1995 to 2000 were used for this analysis as population (Appendix A: Table A1) estimates in the 2001 and 2002 had time series biases and because of the incomplete

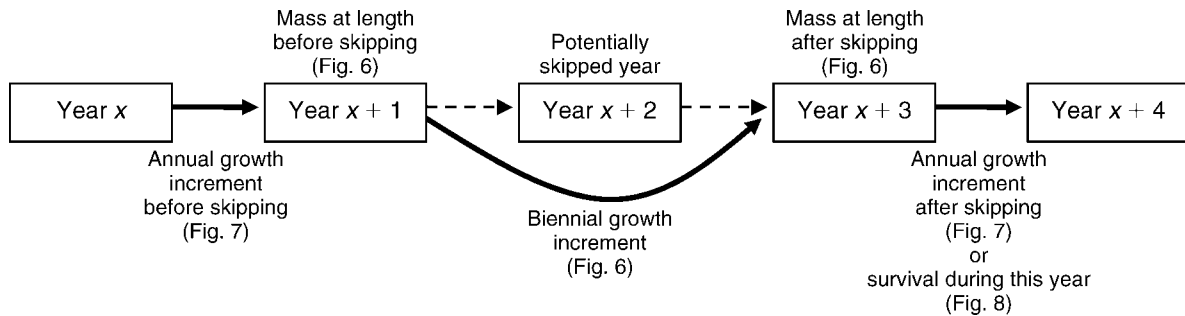


FIG. 1. A depiction of the time periods used for examining differences between bull trout (*Salvelinus confluentus*) that skipped reproductive events and those that did not in Lower Kananaskis Lake, Alberta, Canada.

census in 2001. This analysis was completed for all adult fish and then for first-time spawners only to see whether 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; Fig. 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 of 1995–1997, 1996–1998, 1997–1999, 1998–2000, and 1999–2001 were used (Appendix A: Table A1). The period 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 whether non-repetitive spawners had higher growth rates than fish that spawned repeatedly. We included fish that spawned for three consecutive years vs. fish that had spawned, skipped a year, and then spawned (Fig. 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 were examined for differences between the two strategies (Fig. 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 of 1995–1997, 1996–1998, 1997–1999, 1998–2000, and 1999–2001 were used (Appendix A; 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 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 vs. repetitive spawners was examined using logistic regression analysis (Proc Genmod; SAS Institute 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 whether they survived an additional year (Fig. 1). As a result, only fish alive in 1995–1997 surviving to 1998, fish alive in 1996–1998 surviving to 1999, and fish alive in 1997–1999 surviving to 2000 were used in this analysis due to the incomplete census in 2001 (Appendix A: 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 1995–1996 to 1999–2000 for all fish and only first-time spawners (Appendix A: Table A1) were used for this analysis as population estimates in 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

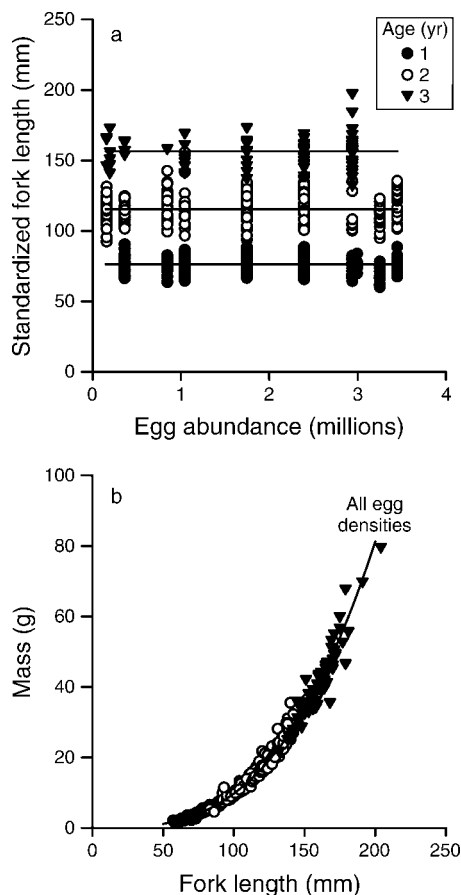


FIG. 2. Growth of juvenile bull trout electrofished in Smith-Dorrien Creek: (a) length at age in relation to egg density and (b) the length–mass relationship. Egg density was found to be insignificant in the length–mass relationship (length–mass, $P = 0.1213$) and not the most parsimonious model in the length-at-age model. Solid lines indicate linear model predictions. Juvenile size was standardized to fork length on 15 August, 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.

of selection, was calculated on an annual basis. Relative fitness is 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 2001) to determine the effects of body length on absolute fitness on linear and nonlinear 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 whether 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 because 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 ($F_{1,566} = 0.01$, $P = 0.9193$, $n = 594$; Fig. 2a, Appendix C: Table C1), although mean size between age classes did vary (Appendix B: 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 (Appendix B: Table B1). Density was not part of the most parsimonious model to describe mass at length (Fig. 2b; Appendix C: Table C2).

In contrast, there was strong evidence that density significantly influenced growth in body size of adult bull trout in Lower Kananaskis Lake (Fig. 3; see Appendix C: Tables C3 and C7 for model selection). Individual annual growth in fork length was inversely related to adult abundance and fish length (Fig. 3a, d; Appendix B: 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 (Fig. 3b, e; Appendix B: Table B1). A residual analysis demonstrated no relationship with length and a normal distribution ($F_{1,1002} = 2.96$, $P = 0.0854$, $n = 2138$; see also Appendix E: Fig. 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 Fig. 3 and Appendix B: 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 Appendix C: Table C11 for model selection). A density-dependent change in mass at length was detected in this study (Fig. 3c, f; Appendix B: Table

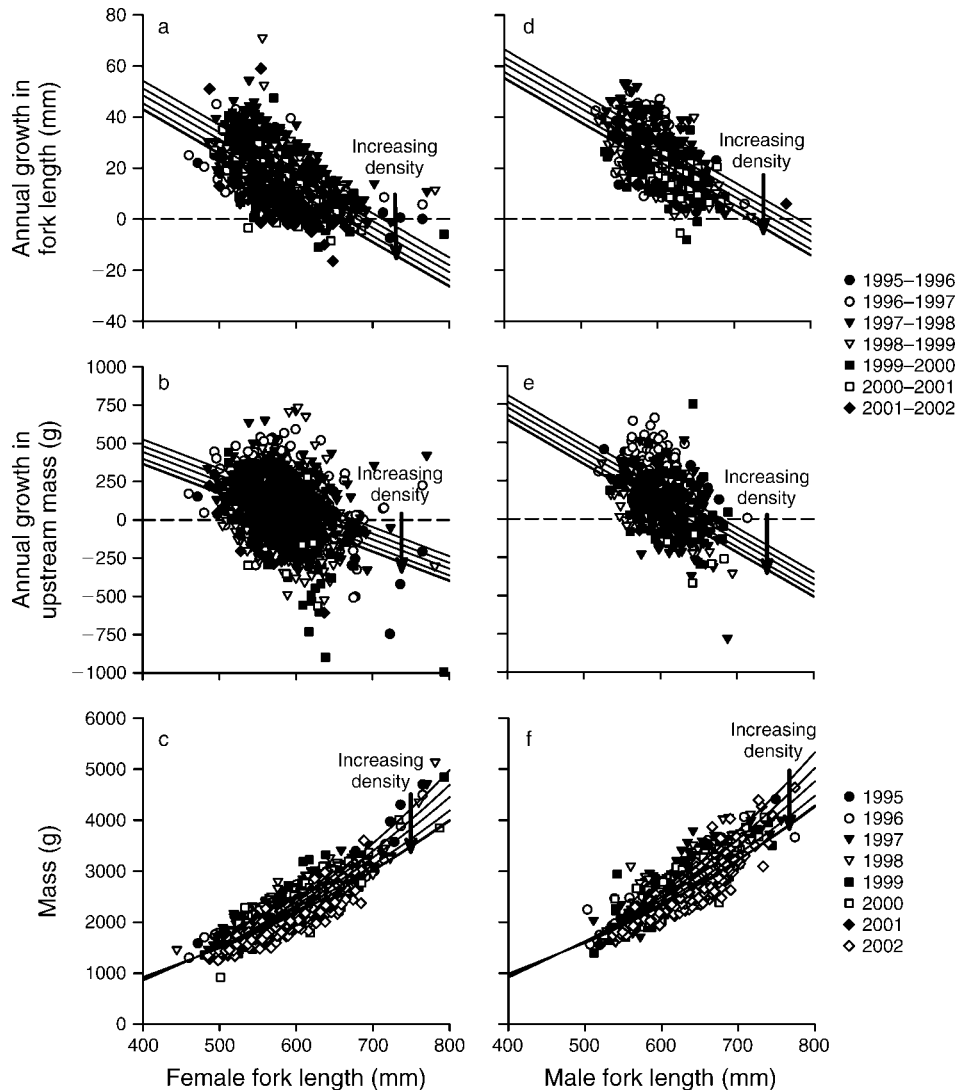


FIG. 3. Annual growth in (a, d) length, (b, e) mass, and (c, f) condition in relation to adult density and gender for adult bull trout in Lower Kananaskis Lake. Solid lines indicate linear model predictions. Repeated measures were accounted for in this analysis. For length, mass, and condition, respectively,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

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 Eq. 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 (Fig. 4; Appendix B: Table B2; see Appendix C: 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 ~19 mm for males and declined by ~11 mm for females when the population experienced an increase of 1500

TABLE 1. Estimates of standard von Bertalanffy growth parameters of bull trout (*Salvelinus confluentus*) calculated from model predictions using Fabens' translation and the allometric parameters of the mass-at-length relationship calculated from model predictions.

Parameter	Estimate
von Bertalanffy growth model: $L_t = L_\infty \times (1 - e^{-K \times (t-t_0)})$	
K	0.1904
Female L_∞	$732.6 - 0.0512 \times \text{adult abundance}$
Male L_∞	$803.3 - 0.0512 \times \text{adult abundance}$
t_0	N/A
Length-mass regression: $M_t = aL_t^b$ or $\ln(M_t) = \ln(a) + b \times \ln(L_t)$	
Female $\ln(a)$	$-9.294 + 0.002099 \times \text{adult abundance}$
Male $\ln(a)$	$-9.227 + 0.002099 \times \text{adult abundance}$
b	$2.674 - 0.00034 \times \text{adult abundance}$

Notes: Abbreviations are: 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; M_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. The study was conducted in Lower Kananaskis Lake, Alberta, Canada.

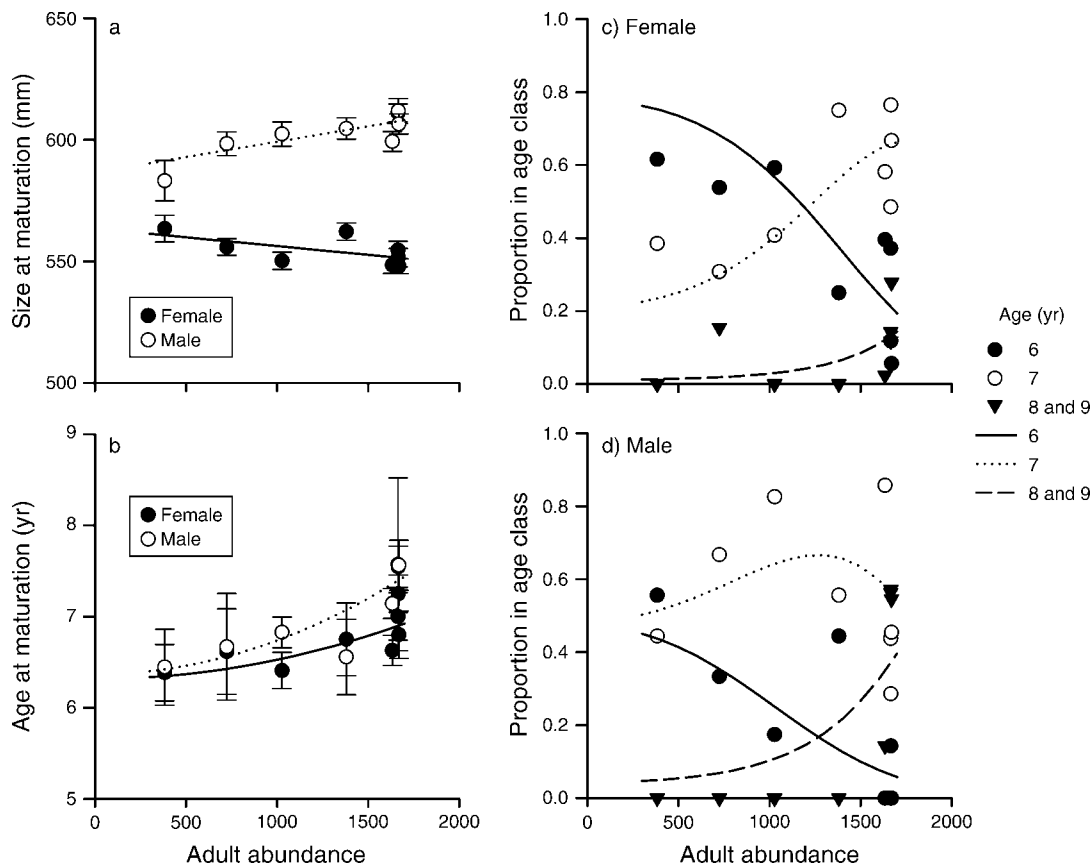


FIG. 4. (a) Size at maturation and (b) age at maturation (mean \pm 95% CL) in relation to total adult abundance and gender for adult bull trout in Lower Kananaskis Lake. Solid lines indicate linear model predictions; $n = 3111$ and 305 for size and age, respectively. (c, d) The relationship between age 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 8–9 yr. Lines represent the model predictions, and the symbols are representative of the data.

TABLE 2. The consequences of density-dependent annual growth to the fecundity and reproductive investment of adult bull trout (*Salvelinus confluentus*) in Lower Kananaskis Lake, Alberta, Canada.

Gender, by density level	Year 1		Year 2		No. eggs produced	Annual growth rate	
	Initial length (mm)	Initial mass (g)	Final length (mm)	Final mass (g)		Length (mm/yr)	Mass (g/yr)
Low (60)							
Female	550	1948	581	2228	4383	31.1	280.3
Male	550	2083	593	2500		43.4	417.1
High (1680)							
Female	50	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

Notes: 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 percentage deviation at low density, positive or negative (indicated by the sign), from the value at carrying capacity.

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, although males delayed maturation longer than females (Fig. 4; Appendix B: 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 (Appendix B: Table B2). These results suggest that the proportion of females maturing at age 6 yr declined, while the proportion of females maturing at age 7 yr or greater than age 7 yr increased with density (Fig. 4). Males generally matured later than females, with similar proportions maturing at age 6 yr or age 7 yr at low densities. As density increased, the proportion of males maturing at age 6 yr declined rapidly, while the proportion maturing at age 7 yr increased slightly. At high densities the number of males maturing at age 6 yr was low, the number maturing at age 7 yr also began to decline, and an increase in the number maturing at age 8 yr was observed (Fig. 4).

Fecundity and reproductive effort

Female fecundity was positively related to fork length (FL, in millimeters) (Johnston et al. 2007) and mass (*M*, in grams; Appendix B: Table B3):

$$E = 1.72 \times 10^{-3} \times (FL)^{2.31} \tag{2}$$

($r^2 = 0.78$, $P < 0.0001$, $n = 26$; Johnston et al. 2007);

$$E = -254.65 + 2.08 \times M \tag{3}$$

($r^2 = 0.80$, $P < 0.0001$, $n = 26$). 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 yr to achieve the

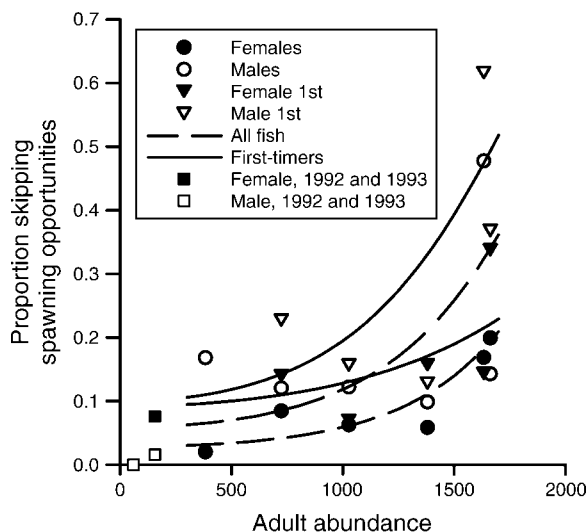


FIG. 5. The proportion of adult bull trout skipping spawning in a given year as a function of gender and adult density in Lower Kananaskis Lake. Lines indicate logistic model predictions: dashed lines represent all fish of a given gender, and solid lines represent only first-time spawners of a given gender. Repeated measures were accounted for in the analysis of all fish. For all fish, $n = 6777$ observations of 2467 individuals, and for first-time spawners, $n = 1604$ observations.

same size that it took a similar-sized male 1 yr 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 (Fig. 5; see Appendix C: Table C16 for model selection; see 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; see 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 at the end of a three-year period (see Appendix C: Tables C4, C8, C12, and C13 for model selection; see Appendix B: Table B4 for the statistical results). Fish that spawned repetitively vs. fish that spawned, skipped spawning, and then spawned again (Fig. 1) had significantly different condition and biennial growth in both fork length and

upstream mass, although this response sometimes varied between the sexes (Fig. 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 (females, $F_{1,1298} = 141.40$, $P < 0.0001$, $n = 1368$; males, $F_{1,496} = 24.97$, $P < 0.0001$, $n = 516$; Fig. 6a). Females that skipped spawning had significantly higher biennial growth rates in fork length than did repetitive spawners ($F_{1,1546} = 68.36$, $P < 0.0001$, $n = 1551$; Fig. 6c). 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 (females, $F_{1,938} = 101.79$, $P < 0.0001$, $n = 1074$; males, $F_{1,406} = 13.63$, $P = 0.0003$, $n = 413$; Fig. 6d). When mass at length was examined again after non-repetitive spawners skipped spawning, it was determined that both genders returned to a heavier mass at length than those that had spawned repeatedly (females, $F_{1,794} = 136.80$, $P < 0.0001$, $n = 1368$; males, $F_{1,374} = 29.61$, $P < 0.0001$, $n = 516$; Fig. 6b).

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 interval when fish potentially did not spawn were examined (Fig. 1; see Appendix C: Tables C5, C6, C9, and C10 for model selection; see Appendix B: Table B4 for statistical results). Females that repetitively spawned had significantly higher annual growth rates in fork length ($F_{1,1086} = 67.65$, $P < 0.0001$, $n = 1308$; Fig. 7a) and in upstream mass ($F_{1,711} = 69.07$, $P < 0.0001$, $n = 1056$; Fig. 7c) 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 ($F_{1,373} = 3.18$, $P = 0.0753$, $n = 415$; Fig. 7a), 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 ($F_{1,311} = 20.40$, $P < 0.0001$, $n = 344$; Fig. 7c). 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 ($F_{1,844} = 1.35$, $P = 0.2455$, $n = 1110$; Fig. 7b), but had significantly lower growth rates in upstream mass ($F_{1,787} = 6.94$, $P = 0.0086$, $n = 958$; Fig. 7d), a result similar to that before they took a year off. However, the difference between spawning strategies was 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 ($F_{1,196} = 5.15$, $P = 0.0243$, $n = 210$; Fig. 7b) but did not have significantly different growth in mass ($F_{1,167} = 2.41$, $P = 0.1222$, $n = 183$; Fig.

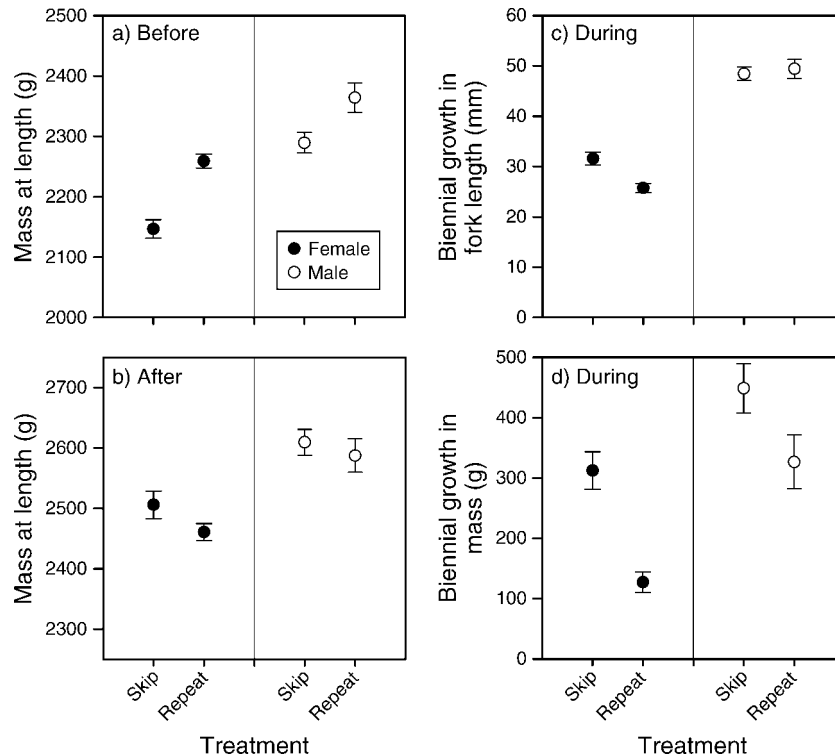


FIG. 6. Condition (a) before and (b) after and biennial growth in (c) length and (d) mass of fish that skip a spawning opportunity in the middle of a three-year interval compared to those that spawned repeatedly for three years, by gender. Least-square means from linear models are presented (mean \pm 95% CL), 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.

7d). 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 (Fig. 1) was found to differ between the two strategies (Fig. 8). Non-repetitive spawners had significantly lower survival than repetitive spawners (see Appendix C: Table C14 for model selection; also see Appendix B: 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 <10% to >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; also see Appendix B: Table B5), although the difference in survival was less (Fig. 8), varying between <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 generally having higher survival than males, were also found (Fig. 8).

Evolution

The opportunity for selection (I) was low (all fish, 0.22 ± 0.13 [mean \pm SD], range 0.11–0.45; first-time

spawners, 0.23 ± 0.21 , range 0.08–0.55), likely because of the relatively high annual survival rate in the earlier years of the study (all fish, 0.83 ± 0.1 , range 0.69–0.90; first-time spawners, 0.83 ± 0.13 , range 0.64–0.93; 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 , range -0.74 to -0.22) suggesting small fish are favored (Appendix F: Table F1). First-time spawners had two insignificant linear coefficients (-0.39 ± 0.26 , range -0.69 to 0.01). Results from the nonlinear 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 of results

The magnitude of the variation of all of the examined life-history traits are illustrated in Fig. 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

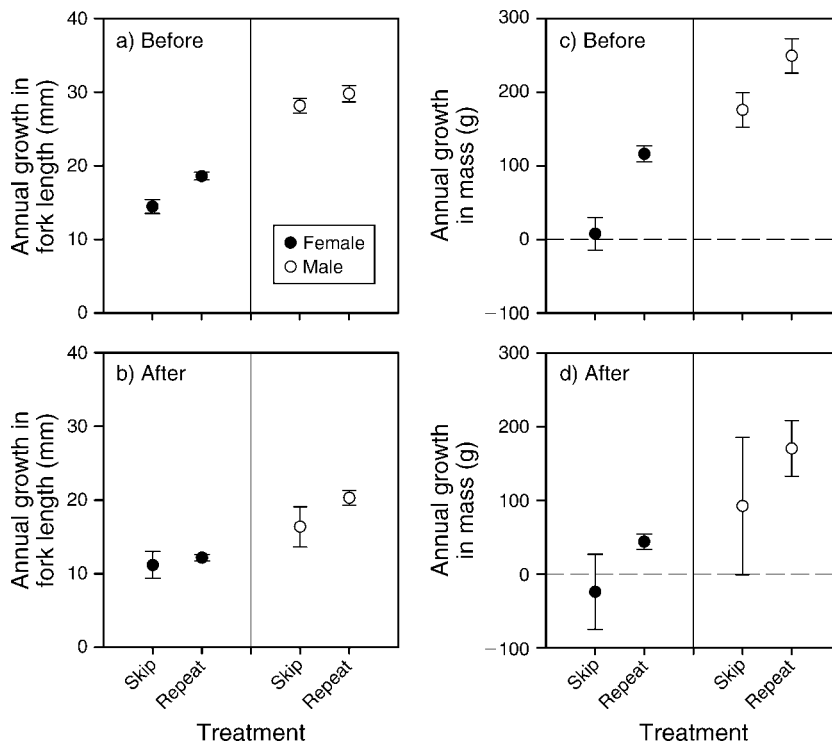


FIG. 7. Annual growth in (a, b) length and (c, d) mass before and after a potentially skipped spawning opportunity for fish that skipped and those that spawned repeatedly, by gender. Least-square means from linear models are presented (mean \pm 95% CL), and all other variables were set equal to their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

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 \sim 85% lower at low density.

DISCUSSION

We observed density-dependent changes in age-dependent survivorship of bull trout in Lower Kananaskis Lake, where the adult population increased 28-fold after the implementation of zero-harvest regulations and approached an apparent carrying capacity (John-

ston 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, Parkinson et al. 2004). Results from this study demonstrate substantial variation in life-history traits that can compensate for harvest (Fig. 9), which has important consequences for 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; Fig. 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 found to be density dependent (Johnston et al. 2007). This is consistent with results found by Elliott (1994) that showed 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 territo-

ries, 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, 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 (Jenkins et al. 1999, Post et al. 1999). In this highly competitive environment, the reduced fitness from density-dependent growth and thus reproduction may change the balance in the trade-offs 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 (Cichoń and Kozłowski 2000). Therefore, large females should spawn despite low energy 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 energy 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 (Fig. 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

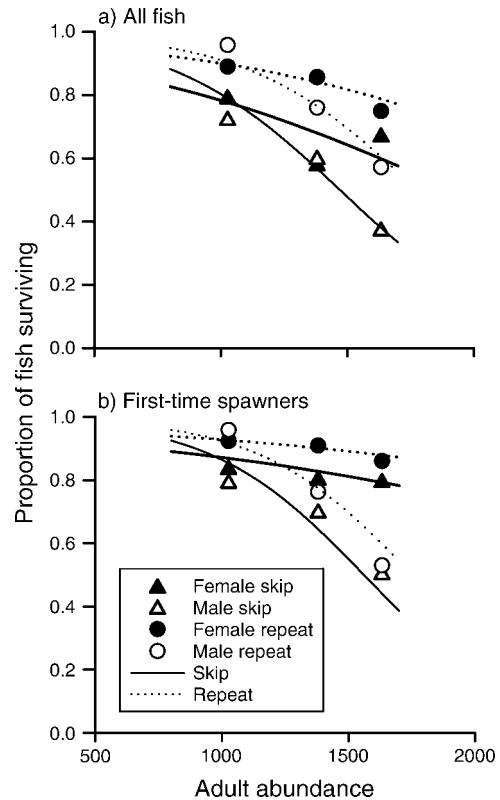


Fig. 8. The proportion of adult bull trout surviving after a potentially skipped spawning opportunity for fish that skipped and those that spawned repeatedly as a function of gender and adult density in Lower Kananaskis Lake. Lines indicate logistic model predictions: solid for alternate spawners and dotted for repeat spawners. (a) All fish and (b) only first-time spawners were examined. For all fish, $n = 1136$ observations, and for first-time spawners, $n = 643$. Note that $P = 0.0649$ for the sex \times density interaction term.

fecundity was responsible for regulating this bull trout population. However, density-dependent changes in growth will affect the mean size of fish in the system and may alter the effectiveness of size-dependent harvest regulations, making younger fish more vulnerable in heavily exploited systems.

Maturation

The timing of maturation represents the compromise between the benefits and costs of growth, 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, Cichoń and Kozłowski 2000,

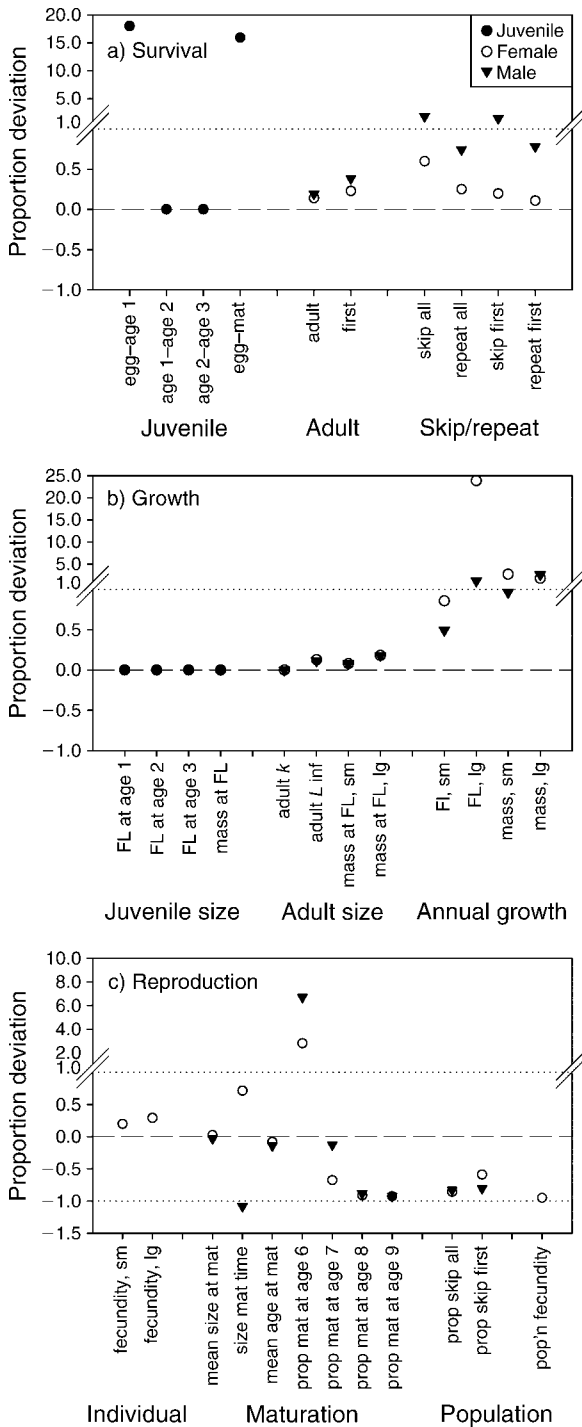


FIG. 9. Compensatory changes in life-history traits: (a) survival; (b) growth; (c) reproduction. This is a comparison of the predictions of the life-history traits examined at low density in relation to carrying capacity. All values represent $(x - K)/|K|$, where K is the value at carrying capacity and x is the value at low density, except for "size mat time" in panel (c). This is the difference in size at maturity $(x - K)$ divided by the annual growth rate at high density. Juvenile and adult survival data are from Johnston et al. (2007). Key for panel (a): first, first-time spawners; skip, skipping spawning; skip all, fish that skipped spawning; repeat all, fish that repeated spawning; skip

Haugen 2000). In Lower Kananaskis Lake, increased density resulted in delayed maturation (approximately one-year change in an eight-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, Engelhard and Heino 2004a, Olsen et al. 2004). 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. However, 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 cannot be determined definitively. Importantly, it cannot 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, which 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 for which 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, Cichoń and Kozłowski 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-

first, fish that skipped spawning the year following the first year they spawned; repeat first, fish that spawned repeatedly for the first two years after maturation. Key for panel (b): FL, fork length; adult k , von Bertalanffy growth model coefficient; L inf, von Bertalanffy growth model L infinity parameter; sm, small fish; lg, large fish. Key for panel (c): mat, maturation; size mat time, time (yr) to make up difference in size at maturation (between low and high density) given growth rate in a high-density environment; prop mat, proportion maturing in a year at age given (yr); prop skip all, proportion of all fish skipping spawning; prop skip first, proportion of first-time spawners skipping spawning; pop'n fecundity, number of eggs produced by all females in the population.

specific response of the Lower Kananaskis Lake bull trout population suggests that these trade-offs 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 that they are likely to achieve given the probability of survival. This threshold may be positively related to the asymptotic size that an individual can attain (Kozłowski 1996, Stamps and Krishnan 1997). Therefore a smaller size at maturation is likely in high-density environments. The timing of energy 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 in which 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 defense 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 a 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 that 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 defense (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 and 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 that are being selected against. 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 to be 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 results of 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 cannot rule out 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 was substantial variation in these traits during the recovery of this population (Fig. 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 reproductive relationships. However, the mechanisms for body-size-dependent reproductive success seem to differ between the genders (i.e., size–fecundity relationships vs. nonrandom mate selection and male–male competition). These sex-specific differences in how life-history characteristics respond to changes in density should be recognized because 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 at maturation, size at maturation, and reproductive characteristics are primarily plastic responses over short timescales. Other studies have also 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 for 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 harvest mortality. Increased individual growth, earlier maturation, more frequent reproduction, and lower mortality at low densities as a result of harvest all act in a compensatory direction. But it is also clear that prior to the imposition of a catch-and-release regulation, 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 such as this one are influenced by processes that are strictly compensatory because there is also a series of harvest-related processes that can act in a depensatory manner (Shuter et al. 1998, Post et al. 2002, 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 that may be counter to the direction of natural selection (Edeline et al. 2007, Jørgensen et al. 2007, Biro and Post 2008, Hutchings and Fraser 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.

ACKNOWLEDGMENTS

We acknowledge the financial support from Challenge Grants in Biodiversity (ACA), TransAlta Utilities, Alberta Sustainable Resource Development, the Alberta Conservation Association, and the Natural Sciences and Engineering Research Council of Canada. We also thank the staff and administration of Kananaskis Country and Peter Lougheed Provincial Park for their support throughout the study, and all the field assistants and volunteers who participated in this study. We are also grateful to the staff of Alberta Sustainable Resource Development and Alberta Conservation Association for their assistance over the years, specifically Jim Stelfox and Brian Lajeunesse. We thank Craig Mushens for developing and managing the early stages of this project. Finally, we thank the

two anonymous reviewers, whose constructive comments helped to improve the quality of this paper.

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APPENDIX A

Summary of data used for the analyses (*Ecological Archives* A019-019-A1).

APPENDIX B

Statistical results for the selected model (*Ecological Archives* A019-019-A2).

APPENDIX C

Repeated-measures and model selection methods and results (*Ecological Archives* A019-019-A3).

APPENDIX D

Multinomial logistic age-at-maturation methods and results (*Ecological Archives* A019-019-A4).

APPENDIX E

Residual plot from analysis of growth in mass (*Ecological Archives* A019-019-A5).

APPENDIX F

Natural selection analyses results (*Ecological Archives* A019-019-A6).

Ecological Archives A019-019-A1

Fiona D. Johnston and John R. Post. 2009. Density-dependent life-history compensation of an iteroparous salmonid. *Ecological Applications* 19:449–467.

Appendix A (TABLE A1). Summary of data used for the analyses.

Analysis	Time period						
	1995	1996	1997	1998	1999	2000	2001
Juvenile length-at-age and condition							
Age-1	56	22	38	39	61	33	
Age-2	40	29	25	15	35	30	
Age-3	6	3	5	1	7	12	
Adult condition							
All years	323	611	939	850	1077	1308	
Before skipping	219	466	416	493	290		
After skipping			226	390	409	673	
Age-at-maturation	22	19	50	17	64	51	
Size-at-maturation	245	385	365	504	424	390	
Proportion skipping							
All fish	357	719	1027	1380	1631	1663	
First-time spawners		223	363	278	465	275	
Time period							
	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002
Annual growth							
Length	221	503	686	637	529	207	
Mass	206	476	568	402	453	12	
Annual growth before skipping							
Length	200	460	587	476			

Mass	189	435	482	294
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Annual growth after skipping

Length	179	449	341	351
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Mass	175	367	279	320
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Proportion surviving after skipping

All fish			227	493	416
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First-time spawners			184	304	155
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Natural Selection

All fish	334	649	939	1277	1150
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First-time spawners	250	391	370	504	427
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Time period

1995–1997	1996–1998	1997–1999	1998–2000	1999–2001
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Biennial growth

Length	227	493	416	774	308
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Mass	219	373	409	463	23
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Ecological Archives A019-019-A2

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Appendix B. Tables of statistical results for selected model.

TABLE B1. Results from the most parsimonious models describing growth of adult bull trout in Lower Kananaskis Lake and juvenile bull trout in Smith-Dorrien Creek. Proc Mixed (SAS Institute Inc. 2001) was used. FL is fork length in mm. Age is in years. Day of the year is when juveniles were captured electrofishing. Egg density is the estimated population fecundity in that year (total egg number in Smith Dorrien Creek). Initial density and density represent adult abundance in Lower Kananaskis Lake. The numerator degrees of freedom (df) was 1 in all cases except for juvenile Age when it was 2, and the denominator df is provided (df_{den}). The R^2 value is the square of the Pearson correlation coefficient of the observed and predicted values with and without density included. See Table A1 for sample sizes used in the analyses. SE = standard error.

Growth model and variables	df _{den}	F value	P > F	Coefficient	Estimate	SE	<i>t</i>
Juvenile growth in length: FL = age + day of year							
Day of year	589	333.9	<0.0001	Day of year slope	0.32	0.02	<1
Age	415	3309.9	<0.0001	Age 1 intercept	2.98	4.05	
				Age 2 intercept	42.09	4.10	<1
				Age 3 intercept	83.01	4.29	<1
Standard deviation: SD = age + eggdensity							
Age	15	22.45	0.0003				
Egg density	15	0.22	0.6461				
Coefficient of variation: CV = age + eggdensity							
Age	15	3.33	0.0878				
Egg density	15	0.02	0.8943				
Juvenile condition: ln(mass) = ln(a) + b × ln(FL)							
Ln(FL)	578	86798.6	<0.0001	ln(a)	-11.82	0.05	<1
				b	3.06	0.01	<1
Adult annual growth in fork length: change in FL = initialFL + sex + initialdensity							
Initial FL	907	1708.96	<0.0001	Female Intercept	127.03	2.42	<1
Sex	1572	832.53	<0.0001	Male Intercept	139.29	2.54	<1
Initial Density	1949	547.05	<0.0001	Initial Density	-0.0089	0.0004	<1
				FL	-0.1734	0.0042	<1
Adult annual growth in upstream mass: change in mass = initialFL + sex + initialdensity + sex × initialFL							
Initial FL	746	412.26	<0.0001	Female Intercept	1336.82	63.63	<1
Sex	735	22.78	<0.0001	Male Intercept	2014.93	127.07	<1

Initial density	1786	212.1	<0.0001	Density	-0.13	0.01	<
Sex × FL	753	17.51	<0.0001	F FL	-1.91	0.11	<
				M FL	-2.89	0.21	<
Adult upstream mass-at-length: $\ln(\text{mass}) = \ln(\text{FL}) + \text{sex} + \text{density} + \ln(\text{FL}) \times \text{density}$							
$\ln(\text{FL})$	6360	3682.24	<0.0001	Female intercept	-9.29	0.28	<
Sex	3143	628.84	<0.0001	Male intercept	-9.23	0.28	<
Density	6369	116.38	<0.0001	Density	0.0021	0.0002	<
$\ln(\text{FL}) \times \text{density}$	6370	122.21	<0.0001	$\ln \text{FL}$	2.67	0.04	<
				$\ln(\text{FL}) \times \text{density}$	-0.00034	0.00003	<

TABLE B2. Results from the most parsimonious model describing the timing of maturation for female and male bull trout in Lower Kananaskis Lake in relation to the abundance of adults (density). Proc GLM and Proc Genmod (SAS Institute Inc. 2001) were used. Age-at-maturation includes both generalized linear model (GLM) results and the more robust multinomial logistic regression results. The R^2 values are from the generalized linear model with and without density. The pseudo R^2 is the correlation between the observed and predicted proportions squared with and without density. The degrees of freedom was 1 in all cases. See Table A1 for sample sizes used in the analyses. Sample sizes were 3111 and 305 fish for size-at-maturation and age-at-maturation respectively. SE = standard error.

Maturation model and variables	F value	$P > F$	Coefficient	Estimate	SE	$P > t $
Size-at-maturation						
Sex	41.31	<0.0001	Female intercept	563.5	2.13	<0.0001
Density	4.51	0.0337	Male intercept	586.5	2.87	<0.0001
Sex × density	60.54	<0.0001	Female density	-0.0072	0.0015	<0.0001
			Male density	0.0127	0.0020	<0.0001
Age-at-maturation GLM						
Sex	0.09	0.7657	Female intercept	6.32	0.11	<0.0001
Density ²	60.21	<0.0001	Male intercept	6.37	0.13	<0.0001
Sex × density ²	4.71	0.0308	Female density	2.10E-07	5.00E-08	<0.0001
			Male density	3.70E-07	6.00E-08	<0.0001
Age-at-maturation multinomial						
	X^2	$P > X^2$	Coefficient	Estimate	SE	$P > t $
Sex	31.06	<0.0001	Female age 6	1.25	0.32	<0.0001
Density ²	51.73	<0.0001	Female age 6+7	4.46	0.42	<0.0001

			Female age 6-8	7.55	0.71	<0.0001
			Male age 6	-0.12	0.32	0.713
			Male age 6+7	3.10	0.37	<0.0001
			Male age 6-8	6.19	0.67	<0.0001
			Density	-9.26E-07	1.36E-07	<0.0001

TABLE B3. Length- and mass-fecundity relationships for female bull trout in Lower Kananaskis Lake. Proc GLM (SAS Institute Inc. 2001) was used. FL is fork length in millimeters and weight was in grams. The numerator degrees of freedom (df) was 1 in both cases and the denominator was 24. The r^2 values are from the GLM. $N = 26$ females that were mortalities in 1999. The length-fecundity relationship was previously reported in Johnston et al. (2007). SE = standard error.

Fecundity model	Variable	F value	P > F	Coefficient	Estimate	df
Length-fecundity: $\ln(\text{Egg \#}) = \ln(\text{FL})$						
	ln(FL)	83.94	<0.0001	intercept	-6.37	1
				slope	2.31	24
Mass-fecundity: $\text{Egg \#} = \text{upstream mass}$						
	Mass	94.61	<0.0001	intercept	-254.7	24
				slope	2.08	24

TABLE B4. Results for the most parsimonious models describing differences in growth of adult bull trout that skipped a reproductive event and those that did not in Lower Kananaskis Lake. Proc Mixed (SAS Institute Inc. 2001) was used. Least-Squared means (LS Means) estimates are provided and all other variables were set equal to their mean values for the computation. The numerator degrees of freedom (df) was 1 in all cases and the denominator df is provided (df_{den}). The R^2 value is the square of the Pearson correlation coefficient of the observed and predicted values with spawning frequency variables (SP) and with only the core model (Core) that was previously found to describe the density-dependent relationship. SE = standard error.

Growth model and variables	df_{den}	F value	P > F	Coefficient	Estimate	SE	R^2
Biennial growth in fork length							
Initial FL	1697	2042.72	<0.0001	Female alternate	31.59	0.65	<0.0001
Sex	1402	601.88	<0.0001	Female repeat	25.71	0.49	<0.0001
Initial density	1916	385.19	<0.0001	Male alternate	48.45	0.68	<0.0001
Spawnfrequency	1838	14.55	0.0001	Male repeat	49.42	0.96	<0.0001
Sex \times spawnfrequency	1578	36.33	<0.0001				
Annual growth in fork length before skipping							

Initial FL	1275	898.99	<0.0001	Female alternate	14.46	0.48	<
Sex	1173	596.48	<0.0001	Female repeat	18.57	0.26	<
Initial density	1673	51.88	<0.0001	Male alternate	28.15	0.52	<
Spawnfrequency	1541	40.32	<0.0001	Male repeat	29.79	0.57	<
Sex × spawnfrequency	1498	8.11	0.0045				
Annual growth in fork length after skipping							
Initial FL	913	444.35	<0.0001	Female alternate	11.18	0.92	<
Sex	996	55.84	<0.0001	Female repeat	12.18	0.22	<
Initial density	1309	326.47	<0.0001	Male alternate	16.36	1.39	<
Spawnfrequency	1015	8.03	0.0047	Male repeat	20.29	0.51	<
Sex × spawnfrequency	999	2.9	0.0891				
Biennial growth in upstream mass							
Initial FL	597	373.53	<0.0001	Female alternate	312.37	15.83	<
Sex	578	13.23	0.0003	Female repeat	127.42	8.57	<
Initial density	591	9.27	0.0024	Male alternate	448.62	20.74	<
Sex × FL	1300	281.34	<0.0001	Male repeat	326.54	22.63	<
Spawnfrequency	667	79.46	<0.0001				
Sex × spawnfrequency	634	3.58	0.0589				
Annual growth in upstream mass before skipping							
Initial FL	459	241.53	<0.0001	Female alternate	7.62	11.37	<
Sex	453	18.46	<0.0001	Female repeat	115.84	5.61	<
Initial density	1274	107.41	<0.0001	Male alternate	175.67	12.01	<
Sex × FL	460	12.27	0.0005	Male repeat	249.02	11.81	<
Spawnfrequency	802	80.09	<0.0001				
Sex × spawnfrequency	778	3.07	0.0799				
Annual growth in upstream mass after skipping							
Initial FL	205	113.86	<0.0001	Female alternate	-23.91	25.98	<
Sex	201	10.23	0.0016	Female repeat	43.96	5.42	<
Initial density	1045	130.54	<0.0001	Male alternate	92.53	47.24	<
Sex × FL	206	8.93	0.0031	Male repeat	170.73	19.07	<
Spawnfrequency	306	7.67	0.006				
Sex × spawnfrequency	305	0.04	0.8447				

Adult upstream mass-at-length before skipping							
Ln(FL)	1819	2222.24	<0.0001	Female alternate	7.67	0.0036	<
Sex	916	166.33	<0.0001	Female repeat	7.72	0.0026	<
Density	1788	1.97	0.1602	Male alternate	7.74	0.0038	<
Ln(FL) × density	1787	2.01	0.1564	Male repeat	7.77	0.0052	<
Spawnfrequency	1148	120.31	<0.0001				
Sex × spawnfrequency	952	7.37	0.0068				
Adult upstream mass-at-length after skipping							
Ln(FL)	1644	129.6	<0.0001	Female alternate	7.83	0.0047	<
Sex	1075	85.62	<0.0001	Female repeat	7.81	0.0029	<
Density	1624	0.38	0.5374	Male alternate	7.87	0.0041	<
Ln(FL) × density	1623	0.25	0.6169	Male repeat	7.86	0.0054	<
Spawnfrequency	1225	10.48	0.0012				
Sex × spawnfrequency	1190	1.49	0.2229				

TABLE B5. Results from the most parsimonious model describing differences in survival of adult bull trout in Lower Kananaskis Lake, between those that skipped a reproductive event and those that did not. In addition the proportion of fish skipping a reproductive event is related to adult abundance. Proc Genmod (SAS Institute Inc. 2001) was used. The pseudo R^2 is the correlation between the observed and predicted proportions squared. The degrees of freedom was 1 in all cases. SE = standard error.

Growth Model	Variable	χ^2	$P > \chi^2$	Coefficient	Estimate	SE
Probability of survival						
All fish	Sex	1.98	0.1591	Female alternate	2.69	0.63
	Density	21.05	<0.0001	Female repeat	3.60	0.63
	Sex × density	25.61	0.0649	Male alternate	4.41	1.09
	Spawnfrequency	3.41	<0.0001	Male repeat	5.32	1.08
				Female density	-0.0014	0.0004
				Male density	-0.0030	0.0008
First-time spawners	Sex	2.2	0.1548	Female alternate	2.81	0.94
	Density	5.53	0.0187	Female repeat	3.44	0.91
	Sex × density	13.93	0.0417	Male alternate	5.15	1.41
	Spawnfrequency	4.15	0.0002	Male repeat	5.78	1.41

				Female density	-0.0009	0.0007
				Male density	-0.0033	0.0010
Probability of skipping						
All fish	Sex	139.88	<0.0001	Female intercept	-3.53	0.14
	Density ²	217.44	<0.0001	Male intercept	-2.77	0.14
				Density	7.63E-07	5.45E-0
First-time spawners	Sex	0.06	0.8116	Female intercept	-2.29	0.23
	Density ²	60.68	<0.0001	Male intercept	-2.21	0.27
	Sex × density ²	7.18	0.0074	Female density	3.73E-07	1.03E-0
				Male density	7.89E-07	1.17E-0

LITERATURE CITED

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Appendix C. Repeated-measures and model selection methods and results.

Repeated measures analysis

The repeated capture of individuals during this study violates the assumption of independence in linear models. It is common for responses to the independent variable to be correlated if it is the same individual providing the response. Statistically this means that the degrees of freedom or number of independent observations is erroneously large.

In order to account for correlation between years due to the recapture of individuals, the variance-covariance matrix structure of the repeated measures was characterized. Maximum likelihood estimation was used to determine which matrix best characterized the structure of the variance and covariance of the data set in Proc Mixed in SAS (SAS Institute 2001). AICc values were then used to determine which matrix was the most appropriate, using the same biological model and the model selection was continued with this variance-covariance matrix. The Kenward-Roger method was then used to modify the denominator degrees of freedom (df_{den}) to appropriately represent the number of independent observations. The new df_{den} incorporates the

information provided by the variance-covariance matrix about correlation in responses. The analysis was carried out in Proc Mixed in SAS (SAS Institute 2001).

The variance-covariance matrices used in the analysis include the null case when all observations are independent such as is assumed in an ANOVA or linear regression. In this case, the variance is constant and the covariance is zero. Compound symmetry (cs) describes the cases where variance is constant as is covariance at some value other than zero. When all variances and covariances are different an unstructured (un) described the data best. The rest of the variance-covariance matrices incorporate temporal differences. If observations are taken sequentially in time or space, one might expect that correlations would be stronger between years with shorter time steps or smaller distances (Littell et al. 1996). The first-order heterogeneous autoregressive matrix (arh (1)) is one variance-covariance matrix that describes this. The final matrix used was a spatial variance-covariance matrix (sp (pow) (year)). Unlike the autoregressive matrix, this assumes unequally spaced repeated measures and therefore must be accompanied by a continuous coordinate variable (Littell et al. 1996), in this case time. The most complicated situation is where all variances and covariances are different. The variance-covariance structure sometimes differed between the sexes, so sex was used as a grouping variable.

Model Selection

Once repeated measures were accounted for using the appropriate variance-covariance matrix, the best fit model was determined. Proc Mixed in SAS, similar to other generalized linear models, produces a statistical probability associated with each model parameter (SAS Institute

2001). It is based on the assumption of normally distributed data, and the F test is used by incorporating the adjusted denominator degrees of freedom. However, due to the large sample sizes associated with this study, the power to detect a statistically significant relationship is high even though the relationship may not be biologically significant. To address this problem, AICc values were used in addition to statistical significance to determine the best fit model.

To maintain a consistent rigorous approach for testing models, a series of candidate models were examined. The candidate models were similar to those used in a backward stepwise regression that incorporated all combinations of two-way interaction terms and a three-way interaction term. The AICc value and the parametric significance of the models were then examined to determine which model had the lowest AICc value and was statistically significant. Delta AICc values (AICc model – AICc minimum) provide a ranking of the candidate models, and a delta AICc of less than 2 suggests that the model has substantial support and should be considered, models with values from 4 to 7 have considerably less support, while a delta AICc of greater than 10 has essentially no support and suggests that it is highly unlikely that the model is the most parsimonious (Burnham and Anderson 2001). The models used and the model selection are described for each analysis in Tables B1 through C15.

When examining differences between fish that spawned repetitively and those that skipped a spawning event, a core model was used to describe the general density-dependent relationship and then the possible combinations of this model with the additional spawning frequency

variable were examined in the same way as above. Since the data set used to examine the effect of spawning frequency on the dependent variable generally involved a smaller data set, in some cases parameters from the core model became statistically insignificant. However, any nonsignificant terms were left in the models examining spawning frequency as they were assumed to best describe all effects other than spawning frequency as it included more years of data and was not constrained to fish that were captured at the beginning and end of a three-year period.

TABLE C1. Model selection results for juvenile growth (length-at-age) analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Juvenile Growth
	Fork Length-at-Age
Time Period	1995–2003
Sample Size	594
Number of Subjects	570
Variance-Covariance Matrix	CS

Description of Independent Variables

ED = Egg Abundance that produced the cohort

C = The day the fish was captured (i.e., of 365 days in a year)

A = Age of the juvenile

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = C + A + ED + A \times C + A \times ED + ED \times C$	4381.9	174	8	$ED + A \times C + A \times ED + ED \times C + A \times ED \times C$
2) $Y = C + A + ED + A \times C + A \times ED$	4321.4	113.5	7	$ED + A \times C + A \times ED + ED \times C$
3) $Y = C + A + ED + A \times C + A \times ED$	4290.1	82.2	6	$ED + A \times C + A \times ED$

$C + A \times ED$				
4) $Y = C + A + ED + A \times$				
$C + ED \times C$	4273.2	65.3	6	$ED + A \times C + ED \times C$
5) $Y = C + A + ED + A \times$				
$ED + ED \times C$	4317.3	109.4	6	$ED + A \times ED + ED \times C$
6) $Y = C + A + ED + A \times$				
C	4241.6	33.7	5	$ED + A \times C$
7) $Y = C + A + ED + ED$				
$\times C$	4266	58.1	5	$ED + ED \times C$
8) $Y = C + A + ED + A \times$				
ED	4285.7	77.8	5	$ED + A \times ED$
9) $Y = C + A + ED$	4234.9	27	4	ED
10) $Y = C + A + C \times A$	4214.6	6.7	4	$C \times A$
11) $Y = C + A$	4207.9	0	3	0
12) $Y = C + ED + C \times ED$	5713.4	1505.5	4	$ED + C \times ED$
13) $Y = C + ED$	5684.2	1476.3	3	0
14) $Y = A + ED + A \times$				
ED	4391.6	183.7	4	$A \times ED$
15) $Y = A + ED$	4342.3	134.4	3	0
16) $Y = C$	5688.3	1480.4	2	0
17) $Y = A$	4468.5	260.6	2	0

18) $Y = ED$ 5770.2 1562.3 2 0

Model Selected

11) Dependent variable = Dayofyear + Age

TABLE C2. Model selection results for juvenile condition (mass-at-age) analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Juvenile Condition
	Mass-at-Length
Time Period	1995–2003
Sample Size	594
Number of Subjects	570
Variance-Covariance Matrix	CS

Description of Independent Variables

ED = Egg Abundance that produced the cohort

L = Ln(Fork Length in that Year)

A = Age of the juvenile

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + ED + A + A \times L + A \times ED + ED \times L + A \times ED \times L$	-1335.9	66.6	8	ED + A + A x L + A x ED + ED x L + A x ED x L
2) $Y = L + ED + A + A \times L + A \times ED + ED \times L$	-1350.7	51.8	7	ED + A + A x L + A x ED + ED x L
3) $Y = L + ED + A + A \times L + A \times ED$	-1359.6	42.9	6	A + A x L + A x ED

L + A x ED					
4)	Y = L + ED + A + A x				ED + A + A x L + ED
	L + ED x L	-1370.6	31.9	6	x L
5)	Y = L + ED + A + A x				ED + A + A x ED + ED
	ED + ED x L	-1352.5	50	6	x L
6)	Y = L + ED + A + ED				
	x L	-1373.4	29.1	5	ED + A + ED x L
7)	Y = L + ED + A + A x				
	ED	-1361	41.5	5	ED + A + A x ED
8)	Y = L + ED + A + A x				
	L	-1381.5	21	5	ED + A + A x L
9)	Y = L + ED + A	-1382.4	20.1	4	ED + A
10)	Y = L + ED + L x ED	-1385.2	17.3	4	
					0
11)	Y = L + ED	-1393.3	9.2	3	
					0
12)	Y = L + A + L x A	-1393.4	9.1	4	A + L x A
13)	Y = L + A	-1393.8	8.7	3	A
14)	Y = ED + A + ED x				
	A	207.3	1609.8	4	
					0
15)	Y = ED + A	218.4	1620.9	3	
					0
16)	Y = A	390.5	1793	2	
					0
17)	Y = ED	1547.6	2950.1	2	
					0

18)	$Y = L$	-1402.5	0	2	0
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Model Selected**18) Dependent variable = Length**

TABLE C3. Model selection results for adult annual growth in fork length analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Annual Growth Increment
	Fork Length
Time Period	1995/96–2001/02
Sample Size	2931
Number of Subjects	1467
Variance-Covariance Matrix	ARH(1)

Description of Independent Variables

D = Density in Initial Year

L = Fork Length in Initial Year

S = Sex

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	19947.05	58.04	8	$D + L \times D + S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S + L \times D + S \times D$	19928.44	39.42	7	$D + L \times S + S \times D$
3) $Y = L + S + D + L \times S + S \times D$	19908.93	19.92	6	$L \times S + S \times D$

4) $Y = L + S + D + L \times D +$ $S \times D$	19921.63	32.62	6	$D + L \times D + S \times D$	
5) $Y = L + S + D + L \times S +$ $L \times D$	19917.23	28.22	6	$D + L \times S + L \times D$	
6) $Y = L + S + D + L \times D$	19909.42	20.41	5	$D + L \times D$	
7) $Y = L + S + D + L \times S$	19896.62	7.61	5	$L \times S$	
8) $Y = L + S + D + S \times D$	19902.12	13.11	5	$S \times D$	
9) $Y = L + S + D$	19889.01	0.00	4		0
10) $Y = L + S + L \times S$	20363.91	474.90	4	$L \times S$	
11) $Y = L + S$	20356.71	467.69	3		0
12) $Y = S + D + S \times D$	21181.71	1292.70	4	$S \times D$	
13) $Y = S + D$	21168.01	1278.99	3		0
14) $Y = L + D + L \times D$	20601.31	712.30	4	$D + L \times D$	
15) $Y = L + D$	20581.21	692.19	3		0
16) $Y = L$	21114.10	1225.09	2		0
17) $Y = S$	21649.50	1760.49	2		0
18) $Y = D$	21330.20	1441.19	2		0

Model Selected

9) **Dependent variable = Length + Sex + Density**

TABLE C4. Model selection results for adult biennial growth in fork length with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Biennial Growth Increment
	Fork Length
Time Period	1995/97–1999/01
Sample Size	2218
Number of Subjects	1357
Variance-Covariance Matrix	ARH(1)

Description of Independent Variables

D = Density in the Year Prior to Skipping

L = Fork Length in Initial Year

S = Sex

SP = If the fish skipped spawning in the middle year

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S$ + $L \times D + S \times D + L \times S \times D$	17250.57	48.55	8	$S + D + L \times S + L \times D$ + $S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S$ + $L \times D + S \times D$	17231.95	29.93	7	$D + L \times S + L \times D + S$ x D
3) $Y = L + S + D + L \times S$	17212.44	10.42	6	L x S

+ S x D					
4) Y = L + S + D + L x D					
+ S x D	17224.44	22.42	6	D + L x D	
5) Y = L + S + D + L x S					
+ L x D	17222.44	20.42	6	D	
6) Y = L + S + D + L x D	17217.73	15.71	5	D	
7) Y = L + S + D + L x S	17204.53	2.51	5		0
8) Y = L + S + D + S x D	17205.23	3.21	5		0
9) Y = L + S + D	17202.02	0.00	4		0
10) Y = L + S + L x S	17495.82	293.80	4		0
11) Y = L + S	17493.01	290.99	3		0
12) Y = S + D + S x D	18567.12	1365.10	4		0
13) Y = S + D	18583.61	1381.59	3		0
14) Y = L + D + L x D	17810.42	608.40	4	L x D	
15) Y = L + D	17790.01	587.99	3		0
16) Y = L	18125.11	923.09	2		0
17) Y = S	18959.21	1757.19	2		0
18) Y = D	18646.11	1444.09	2		0

Core Model Selected

9) Dependent variable = Length + Sex + Density

Model for Spawning		delta	No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times$				$\text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times$
$\text{D} \times \text{SP}$	17158.18	29.54	9	$\text{D} \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$	17140.87	12.23	8	0
21) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP}$	17134.45	5.81	7	$\text{L} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{D} \times \text{SP}$	17162.05	33.41	7	0
23) $Y = \text{Core} + \text{SP} + \text{S} \times$				
$\text{SP} + \text{D} \times \text{SP}$	17137.75	9.11	7	SP
24) $Y = \text{Core} + \text{SP} + \text{L} \times$				
SP	17160.44	31.80	6	0
25) $Y = \text{Core} + \text{SP} + \text{S} \times$				
SP	17128.64	0.00	6	0
26) $Y = \text{Core} + \text{SP} + \text{D} \times$				
SP	17170.04	41.40	6	SP
27) $Y = \text{Core} + \text{SP}$	17164.13	35.49	5	0
28) $Y = \text{Core}$	17202.02	73.38	4	0

Model Selected

25) Dependent Variable = Core + Spawnfrequency + Sex x Spawnfrequency

TABLE C5. Model selection results for adult annual growth in fork length before skipping with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Annual Growth Increment Before Skipping
	Fork Length
Time Period	1995/96–1998/99
Sample Size	1723
Number of Subjects	983
Variance-Covariance Matrix	ARH(1)

Description of Independent Variables

Density = Density in Initial Year

Length = Fork Length in Initial Year

S = Sex

SP = If the fish skipped spawning after this year of growth

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	11875.68	51.65	8	$S + D + L \times S + L \times D + S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S + L \times D + S \times D$	11855.17	31.13	7	$D + L \times D$
3) $Y = L + S + D + L \times S$	11832.65	8.61	6	0

+ S x D

4) $Y = L + S + D + L \times D$

+ S x D 11858.95 34.91 6 D + L x D + S x D

5) $Y = L + S + D + L \times S$

+ L x D 11846.65 22.61 6 D + L x D

6) $Y = L + S + D + L \times D$ 11847.73 23.70 5 D + L x D

7) $Y = L + S + D + L \times S$ 11824.03 0.00 5 0

8) $Y = L + S + D + S \times D$ 11836.73 12.70 5 S x D

9) $Y = L + S + D$ 11825.32 1.29 4 0

10) $Y = L + S + L \times S$ 11883.02 58.99 4 0

11) $Y = L + S$ 11884.01 59.98 3 0

12) $Y = S + D + S \times D$ 12596.02 771.99 4 S x D

13) $Y = S + D$ 12583.81 759.78 3 0

14) $Y = L + D + L \times D$ 12270.42 446.39 4 D + L x D

15) $Y = L + D$ 12248.11 424.08 3 0

16) $Y = L$ 12354.61 530.57 2 0

17) $Y = S$ 12699.51 875.47 2 0

18) $Y = D$ 12690.31 866.27 2 0

Core Model Selected

7) **Dependent variable = Length + Sex + Density + Length x Sex**

Note: Model 9 was used for further analyses, as we are interested in the difference between

fish that skipped spawning and those that spawned repetitively. Therefore, we only wanted to account for the general density-dependent trend as the core model. The delta AICc value is not greater than 2, and this core model is consistent with the other growth in length models.

Model for Spawning	delta		No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + L \times$				
$\text{SP} + S \times \text{SP} + D \times \text{SP} + S \times$				$\text{SP} + L \times \text{SP} + S \times \text{SP}$
$D \times \text{SP}$	11805.61	39.66	9	$+ D \times \text{SP} + S \times D \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + L \times$				
$\text{SP} + S \times \text{SP} + D \times \text{SP}$	11786.08	20.14	8	$\text{SP} + L \times \text{SP} + D \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + L \times$				
$\text{SP} + S \times \text{SP}$	11772.87	6.92	7	$\text{SP} + L \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + L \times$				
$\text{SP} + D \times \text{SP}$	11790.87	24.92	7	$D \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + S \times$				
$\text{SP} + D \times \text{SP}$	11779.17	13.22	7	$\text{SP} + D \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + L \times$				
SP	11777.85	11.90	6	0
25) $Y = \text{Core} + \text{SP} + S \times$	11765.95	0.00	6	0

SP

26) $Y = \text{Core} + \text{SP} + \text{D} \times$

SP	11786.25	20.30	6	SP + D x SP
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27) $Y = \text{Core} + \text{SP}$	11773.53	7.59	5	0
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28) $Y = \text{Core}$	11827.02	61.07	4	0
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Model Selected
25) Dependent Variable = Core + Spawnfrequency + Sex x Spawnfrequency

TABLE C6. Model selection results for adult annual growth in fork length after skipping with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Annual Growth Increment After Skipping Fork Length
Time Period	1996/97–1999/00
Sample Size	1320
Number of Subjects	793
Variance-Covariance Matrix	ARH(1)

Description of Independent Variables

Density = Density in Initial Year

Length = Fork Length in Initial Year

S = Sex

SP = If the fish skipped spawning before this year of growth

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	8718.61	56.28	8	$S + D + L \times S + L \times D + S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S + L \times D + S \times D$	8699.49	37.15	7	$L \times S + L \times D + S \times D$
3) $Y = L + S + D + L \times S$	8679.06	16.73	6	$S + L \times S + S \times D$

+ S x D

4) $Y = L + S + D + L \times D$

+ S x D	8693.56	31.23	6	L x D + S x D	
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5) $Y = L + S + D + L \times S$

+ L x D	8688.36	26.03	6	L x S + L x D	
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6) $Y = L + S + D + L \times D$	8681.85	19.52	5	L x D	
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7) $Y = L + S + D + L \times S$	8669.15	6.82	5	S + L x S	
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8) $Y = L + S + D + S \times D$	8673.15	10.82	5	S x D	
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9) $Y = L + S + D$	8662.33	0.00	4		0
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10) $Y = L + S + L \times S$	8919.83	257.50	4		0
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11) $Y = L + S$	8917.62	255.29	3		0
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12) $Y = S + D + S \times D$	9063.43	401.10	4	S + S x D	
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13) $Y = S + D$	9050.82	388.49	3		0
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14) $Y = L + D + L \times D$	8862.73	200.40	4	L x D	
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15) $Y = L + D$	8843.92	181.59	3		0
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16) $Y = L$	9140.11	477.78	2		0
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17) $Y = S$	9148.21	485.88	2		0
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18) $Y = D$	9089.61	427.28	2		0
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Core Model Selected

9) Dependent Variable = Length + Sex + Density

Model for Spawning	delta		No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times$				$\text{S} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times$
$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times$				$\text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times$
$\text{D} \times \text{SP}$	8691.24	37.57	9	SP
20) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$	8672.51	18.85	8	$\text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP}$	8660.49	6.82	7	$\text{SP} + \text{L} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{D} \times \text{SP}$	8677.49	23.82	7	$\text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + \text{S} \times$				
$\text{SP} + \text{D} \times \text{SP}$	8665.79	12.12	7	$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + \text{L} \times$				
SP	8665.46	11.80	6	$\text{SP} + \text{L} \times \text{SP}$
25) $Y = \text{Core} + \text{SP} + \text{S} \times$				
SP	8653.66	0.00	6	$\text{S} \times \text{SP}$
26) $Y = \text{Core} + \text{SP} + \text{D} \times$				
SP	8669.56	15.90	6	$\text{SP} + \text{D} \times \text{SP}$
27) $Y = \text{Core} + \text{SP}$	8657.45	3.78	5	0
28) $Y = \text{Core}$	8662.33	8.67	4	0

Model Selected

25) Dependent Variable = Core + Spawnfrequency + Sex x Spawnfrequency

Note: Sex x Spawnfrequency is insignificant - $P = 0.0891$

TABLE C7. Model selection results for adult annual growth in upstream mass analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Annual Growth Increment			
	Upstream Mass			
Time Period	1995/96–2001/02			
Sample Size	2138			
Number of Subjects	1467			
Variance-Covariance Matrix	ARH(1) group = sex			
Description of Independent Variables				
D = Density in Initial Year				
L = Fork Length in Initial Year				
S = Sex				
Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	27797.27	34.64	8	$D + L \times D + S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S + L \times D + S \times D$	27783.65	21.02	7	$D + L \times D + S \times D$
3) $Y = L + S + D + L \times S + S \times D$	27766.84	4.21	6	$S \times D$

4) $Y = L + S + D + L \times D +$ $S \times D$	27796.04	33.41	6	$D + L \times D$	
5) $Y = L + S + D + L \times S +$ $L \times D$	27778.84	16.21	6	$D + L \times D$	
6) $Y = L + S + D + L \times D$	27792.73	30.10	5	$D + L \times D$	
7) $Y = L + S + D + L \times S$	27762.63	0.00	5		0
8) $Y = L + S + D + S \times D$	27779.73	17.10	5		0
9) $Y = L + S + D$	27777.52	14.89	4		0
10) $Y = L + S + L \times S$	27947.02	184.39	4		0
11) $Y = L + S$	27958.21	195.58	3		0
12) $Y = S + D + S \times D$	28169.62	406.99	4	$S \times D$	
13) $Y = S + D$	28165.41	402.78	3		0
14) $Y = L + D + L \times D$	27859.62	96.99	4	$D + L \times D$	
15) $Y = L + D$	27843.91	81.28	3		0
16) $Y = L$	28008.61	245.98	2		0
17) $Y = S$	28409.21	646.58	2		0
18) $Y = D$	28170.61	407.98	2		0

Model Selected

7) **Dependent variable = Length + Sex + Density + Length x Sex**

TABLE C8. Model selection results for adult biennial growth in upstream mass with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Biennial Growth Increment			
	Upstream Mass			
Time Period	1995/97–1999/01			
Sample Size	1487			
Number of Subjects	1357			
Variance-Covariance Matrix	ARH(1) group = sex			
Description of Independent Variables				
D = Density in the Year Prior to Skipping				
L = Fork Length in Initial Year				
S = Sex				
SP = If the fish skipped spawning in the middle year				
Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S$ $+ L \times D + S \times D + L \times S \times D$	20570.20	32.26	8	$S + D + L \times S + L \times D$ $+ S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S$ $+ L \times D + S \times D$	20568.68	30.74	7	$L \times D + S \times D$
3) $Y = L + S + D + L \times S$	20543.26	5.32	6	$S \times D$

+ S x D

4) $Y = L + S + D + L \times D$

+ S x D	20565.36	27.42	6	D + L x D + S x D	
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5) $Y = L + S + D + L \times S$

+ L x D	20552.26	14.32	6	L x D	
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6) $Y = L + S + D + L \times D$	20559.54	21.60	5	D + L x D	
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7) $Y = L + S + D + L \times S$	20537.94	0.00	5		0
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8) $Y = L + S + D + S \times D$	20550.14	12.20	5	S x D	
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9) $Y = L + S + D$	20544.03	6.09	4		0
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10) $Y = L + S + L \times S$	20706.13	168.19	4		0
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11) $Y = L + S$	20722.62	184.68	3		0
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12) $Y = S + D + S \times D$	20875.73	337.79	4		0
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13) $Y = S + D$	20876.22	338.28	3		0
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14) $Y = L + D + L \times D$	20677.73	139.79	4		0
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15) $Y = L + D$	20672.02	134.08	3		0
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16) $Y = L$	20817.51	279.57	2		0
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17) $Y = S$	21095.41	557.47	2		0
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18) $Y = D$	20901.81	363.87	2		0
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Core Model Selected

7) **Dependent variable = Length + Sex + Density + Length x Sex**

Model for Spawning	AICc	delta AICc	No. Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$	20420.15	9.57	10	$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$	20414.02	3.45	9	$\text{SP} + \text{L} \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$	20411.70	1.12	8	$\text{SP} + \text{L} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$	20425.10	14.52	8	$\text{SP} + \text{L} \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$	20412.40	1.82	8	$\text{SP} + \text{S} \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$	20422.88	12.30	7	$\text{SP} + \text{L} \times \text{SP}$
25) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$	20410.58	0.00	7	$\text{S} \times \text{SP}$
26) $Y = \text{Core} + \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{SP}$	20422.98	12.40	7	SP
27) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$	20420.96	10.38	6	0
28) $Y = \text{Core} + \text{L} \times \text{SP}$	20537.94	127.36	5	0

Model Selected

25) Dependent Variable = Core + Spawnfrequency + Sex x Spawnfrequency

Note: Sex x Spawnfrequency is insignificant – $P = 0.0589$

TABLE C9. Model selection results for adult annual growth in upstream mass before skipping with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Annual Growth Increment Before Skipping
	Upstream Mass
Time Period	1995/96–1998/99
Sample Size	1400
Number of Subjects	983
Variance-Covariance Matrix	ARH(1) group = sex

Description of Independent Variables

Density = Density in Initial Year

Length = Fork Length in Initial Year

S = Sex

SP = If the fish skipped spawning after this year of growth

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	18130.30	35.76	8	$S + D + L \times S + L \times D + S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S + L \times D + S \times D$	18116.78	22.24	7	$L \times D + S \times D$
3) $Y = L + S + D + L \times S$	18100.96	6.42	6	$S \times D$

+ S x D

4) $Y = L + S + D + L \times D$

+ S x D	18127.36	32.82	6	D + L x D + S x D	
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5) $Y = L + S + D + L \times S$

+ L x D	18110.56	16.02	6	D + L x D	
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6) $Y = L + S + D + L \times D$ 18122.24 27.70 5 D + L x D

7) $Y = L + S + D + L \times S$ 18094.54 0.00 5 0

8) $Y = L + S + D + S \times D$ 18111.24 16.70 5 S x D

9) $Y = L + S + D$ 18106.03 11.49 4 0

10) $Y = L + S + L \times S$ 18224.83 130.29 4 0

11) $Y = L + S$ 18236.42 141.87 3 0

12) $Y = S + D + S \times D$ 18387.53 292.99 4 S x D

13) $Y = S + D$ 18383.22 288.67 3 0

14) $Y = L + D + L \times D$ 18204.53 109.99 4 D + L x D

15) $Y = L + D$ 18188.22 93.67 3 0

16) $Y = L$ 18298.81 204.27 2 0

17) $Y = S$ 18537.21 442.67 2 0

18) $Y = D$ 18396.91 302.37 2 0

Core Model Selected

7) **Dependent variable = Length + Sex + Density + Length x Sex**

Model for Spawning		delta	No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times$				$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$
$\text{D} \times \text{SP}$	18014.46	19.48	10	$+ \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + \text{L} \times$				$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$
$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$	18004.73	9.75	9	$+ \text{D} \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{S} \times \text{SP}$	17997.80	2.82	8	$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times$				
$\text{SP} + \text{D} \times \text{SP}$	18013.10	18.12	8	$\text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + \text{S} \times$				
$\text{SP} + \text{D} \times \text{SP}$	18001.90	6.92	8	$\text{S} \times \text{SP} + \text{D} \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + \text{L} \times$				
SP	18006.38	11.40	7	$\text{SP} + \text{L} \times \text{SP}$
25) $Y = \text{Core} + \text{SP} + \text{S} \times$				
SP	17994.98	0.00	7	$\text{S} \times \text{SP}$
26) $Y = \text{Core} + \text{SP} + \text{D} \times$				
SP	18010.38	15.40	7	$\text{D} \times \text{SP}$
27) $Y = \text{Core} + \text{SP}$	18003.66	8.68	6	0
28) $Y = \text{Core}$	18094.54	99.56	5	0

Model Selected

25) Dependent Variable = Core + Spawnfrequency + Sex x Spawnfrequency

Note: Sex x Spawnfrequency is insignificant – $P = 0.0799$

TABLE C10. Model selection results for adult annual growth in upstream mass after skipping with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Adult Annual Growth Increment After Skipping
	Upstream Mass
Time Period	1996/97–1999/00
Sample Size	1141
Number of Subjects	793
Variance-Covariance Matrix	ARH(1) group = sex

Description of Independent Variables

Density = Density in Initial Year

Length = Fork Length in Initial Year

S = Sex

SP = If the fish skipped spawning before this year of growth

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	14954.13	19.77	8	D + L x D
2) $Y = L + S + D + L \times S + L \times D + S \times D$	14947.40	13.05	7	D + L x D
3) $Y = L + S + D + L \times S +$	14935.07	0.72	6	0

S x D

4) $Y = L + S + D + L \times D +$

S x D	14959.17	24.82	6	S + D + L x D	
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5) $Y = L + S + D + L \times S +$

L x D	14948.47	14.12	6	D + L x D	
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6) $Y = L + S + D + L \times D$

7) $Y = L + S + D + L \times S$	14934.35	0.00	5		0
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8) $Y = L + S + D + S \times D$

9) $Y = L + S + D$	14943.84	9.48	4		0
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10) $Y = L + S + L \times S$

11) $Y = L + S$	15054.52	120.17	3		0
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12) $Y = S + D + S \times D$

13) $Y = S + D$	15134.82	200.47	3	S	
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14) $Y = L + D + L \times D$

15) $Y = L + D$	14974.52	40.17	3		0
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16) $Y = L$

17) $Y = S$	15235.11	300.76	2	S	
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18) $Y = D$

Core Model Selected

7) **Dependent variable = Length + Sex + Density + Length x Sex**

Model for Spawning		delta	No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$	14918.59	7.50	10	$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{S} \times \text{SP} + \text{D} \times \text{SP}$	14917.56	6.46	9	$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{S} \times \text{SP}$	14912.43	1.33	8	$\text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{D} \times \text{SP}$	14925.33	14.23	8	$\text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP}$ + $\text{D} \times \text{SP}$	14916.23	5.13	8	$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$	14920.20	9.10	7	$\text{SP} + \text{L} \times \text{SP}$
25) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP}$	14911.10	0.00	7	$\text{S} \times \text{SP}$
26) $Y = \text{Core} + \text{SP} + \text{D} \times \text{SP}$	14924.00	12.90	7	$\text{SP} + \text{D} \times \text{SP}$
27) $Y = \text{Core} + \text{SP}$	14918.87	7.78	6	0
28) $Y = \text{Core}$	14934.35	23.25	5	0

Model Selected

25) Dependent Variable = Core + Spawnfrequency + Sex x Spawnfrequency

Note: Sex x Spawnfrequency is insignificant – $P = 0.8447$. However, this model selection

is consistent with the model selected in the other growth in mass analyses and allows for comparison

TABLE C11. Model selection results for adult upstream weight-at-length analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Upstream Condition			
	Mass-at-Length			
	1995–			
Time Period	2002			
Sample Size	6405			
Number of Subjects	3263			
Variance-Covariance Matrix	SP(POW) year, group = sex			
Description of Independent Variables				
D = Density in that Year				
L = Ln(Fork Length in that Year)				
S = Sex				
		delta	No.	
Model	AICc	AICc	Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S +$ $L \times D + S \times D + L \times S \times D$	-16287.78	20.01	8	0
2) $Y = L + S + D + L \times S +$ $L \times D + S \times D$	-16278.48	29.31	7	S + L x S + S x D
3) $Y = L + S + D + L \times S +$	-16188.19	119.60	6	S + L x S + S x D

S x D

4) $Y = L + S + D + L \times D +$

S x D -16285.49 22.30 6 S x D

5) $Y = L + S + D + L \times S +$

L x D -16300.59 7.20 6 S + L x S

6) $Y = L + S + D + L \times D$ -16307.79 0.00 5 0

7) $Y = L + S + D + L \times S$ -16208.79 99.00 5 S + L x S

8) $Y = L + S + D + S \times D$ -16195.09 112.70 5 0

9) $Y = L + S + D$ -16215.09 92.70 4 0

10) $Y = L + S + L \times S$ -15869.39 438.40 4 0

11) $Y = L + S$ -15871.50 436.29 3 0

12) $Y = S + D + S \times D$ -8285.59 8022.20 4 0

13) $Y = S + D$ -8304.40 8003.39 3 0

14) $Y = L + D + L \times D$ -15736.29 571.50 4 0

15) $Y = L + D$ -15684.80 622.99 3 0

16) $Y = L$ -15299.80 1007.99 2 0

17) $Y = S$ -7937.30 8370.49 2 0

18) $Y = D$ -7149.40 9158.39 2 0

Model Selected**6) Dependent variable = Length + Sex + Density + Length x Density**

TABLE C12. Model selection results for adult upstream weight-at-length before skipping with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Upstream Condition Before Skipping			
	Mass-at-Length			
	1995–			
Time Period	1999			
Sample Size	1884			
Number of Subjects	1357			
Variance-Covariance Matrix	SP(POW) year, group = sex			
Description of Independent Variables				
D = Density in that Year				
L = Ln(Fork Length in that Year)				
S = Sex				
SP = If the fish skipped spawning the year after this one				
Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S +$ $L \times D + S \times D + L \times S \times D$	-5113.72	56.86	8	$S + D + L \times S + L \times D$ $+ S \times D + L \times S \times D$
2) $Y = L + S + D + L \times S +$ $L \times D + S \times D$	-5126.34	44.24	7	$L \times D + S \times D$

3) $Y = L + S + D + L \times S +$ $S \times D$	-5141.06	29.52	6	$S \times D$	
4) $Y = L + S + D + L \times D +$ $S \times D$	-5132.06	38.52	6	$D + L \times D + S \times D$	
5) $Y = L + S + D + L \times S +$ $L \times D$	-5149.46	21.12	6	$D + L \times D$	
6) $Y = L + S + D + L \times D$	-5155.17	15.41	5	$D + L \times D$	
7) $Y = L + S + D + L \times S$	-5164.57	6.01	5		0
8) $Y = L + S + D + S \times D$	-5146.87	23.71	5	$S \times D$	
9) $Y = L + S + D$	-5170.58	0.00	4		0
10) $Y = L + S + L \times S$	-5160.78	9.80	4		0
11) $Y = L + S$	-5166.89	3.69	3		0
12) $Y = S + D + S \times D$	-2075.28	3095.30	4	$S \times D$	
13) $Y = S + D$	-2096.79	3073.79	3		0
14) $Y = L + D + L \times D$	-5074.18	96.40	4	$D + L \times D$	
15) $Y = L + D$	-5093.19	77.39	3		0
16) $Y = L$	-5080.59	89.99	2		0
17) $Y = S$	-1794.19	3376.39	2		0
18) $Y = D$	-1862.99	3307.59	2		0

Core Model Selected

9) **Dependent variable = Length + Sex + Density**

Note: Model 6 was used for further analyses, as we are interested in the difference between fish that skipped spawning and those that spawned repetitively. Therefore, we only wanted to account for the general density-dependent trend as the core model which we found for the larger data set in the Table C7.

Model for Spawning	delta		No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$ SP	-5219.98	74.57	10	$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{S} \times \text{SP} + \text{D} \times \text{SP}$	-5262.70	31.85	9	$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{S} \times \text{SP}$	-5286.32	8.23	8	$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$ + $\text{D} \times \text{SP}$	-5264.82	29.73	8	$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP} + \text{D} \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP}$ + $\text{D} \times \text{SP}$	-5268.12	26.43	8	$\text{D} + \text{L} \times \text{D} + \text{D} \times \text{SP} + \text{S} \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$	-5288.14	6.41	7	$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
25) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP}$	-5291.64	2.91	7	$\text{D} + \text{L} \times \text{D} + \text{S} \times \text{SP}$

26) $Y = \text{Core} + \text{SP} + \text{D} \times \text{SP}$	-5271.14	23.41	7	$\text{D} + \text{L} \times \text{D} + \text{D} \times \text{SP}$	
27) $Y = \text{Core} + \text{SP}$	-5294.56	0.00	6	$\text{D} + \text{L} \times \text{D}$	
28) $Y = \text{Core}$	-5155.17	139.39	5		0

Model Selected

27) Dependent Variable = Core + Spawnfrequency

TABLE C13. Model selection results for adult upstream weight-at-length after skipping with spawning frequency analyses. A mixed model was used (Proc Mixed SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Upstream Condition After Skipping
	Mass-at-Length
Time Period	1997–2001
Sample Size	1721
Number of Subjects	1357
Variance-Covariance Matrix	SP(POW) year, group = sex

Description of Independent Variables

D = Density in that Year

L = Ln(Fork Length in that Year)

S = Sex

SP = If the fish skipped spawning the year before this one

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = L + S + D + L \times S + L \times D + S \times D + L \times S \times D$	-4382.42	50.06	8	D + L x D
2) $Y = L + S + D + L \times S + L \times D + S \times D$	-4391.03	41.44	7	S + D + L x S + L x D + S x D
3) $Y = L + S + D + L \times S + L \times D + S \times D$	-4407.25	25.23	6	S + L x S + S x D

S x D

4) $Y = L + S + D + L \times D +$

S x D -4396.05 36.43 6 D + L x D + S x D

5) $Y = L + S + D + L \times S +$

L x D -4409.95 22.53 6 S + D + L x S + L x D

6) $Y = L + S + D + L \times D$ -4414.77 17.71 5 D + L x D

7) $Y = L + S + D + L \times S$ -4427.57 4.91 5 S + L x S

8) $Y = L + S + D + S \times D$ -4412.37 20.11 5 S x D

9) $Y = L + S + D$ -4432.48 0.00 4 0

10) $Y = L + S + L \times S$ -4311.78 120.70 4 S + L x S

11) $Y = L + S$ -4314.79 117.69 3 0

12) $Y = S + D + S \times D$ -2668.28 1764.20 4 D + S x D

13) $Y = S + D$ -2686.39 1746.09 3 D

14) $Y = L + D + L \times D$ -4317.68 114.80 4 0

15) $Y = L + D$ -4329.19 103.29 3 0

16) $Y = L$ -4228.89 203.58 2 0

17) $Y = S$ -2709.09 1723.38 2 0

18) $Y = D$ -2204.39 2228.08 2 D

Core Model Selected**9) Dependent variable = Length + Sex + Density**

Note: Model 6 was used for further analyses, as we are interested in the difference between

fish that skipped spawning and those that spawned repetitively. Therefore, we only wanted to account for the general density-dependent trend as the core model which we found for the larger data set in the Table C7.

Model for Spawning		delta	No.	
Frequency	AICc	AICc	Param.	Nonsignificant Terms
19) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$				
+ $\text{S} \times \text{SP} + \text{D} \times \text{SP} + \text{S} \times \text{D} \times \text{SP}$				$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP}$
	-4347.07	68.48	10	$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
20) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$				$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP}$
+ $\text{S} \times \text{SP} + \text{D} \times \text{SP}$	-4380.99	34.56	9	$\text{SP} + \text{S} \times \text{SP} + \text{D} \times \text{SP}$
21) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$				$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP}$
+ $\text{S} \times \text{SP}$	-4403.12	12.44	8	$\text{SP} + \text{S} \times \text{SP}$
22) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$				$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP}$
+ $\text{D} \times \text{SP}$	-4390.32	25.24	8	$\text{SP} + \text{D} \times \text{SP}$
23) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP}$				$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{S} \times \text{SP}$
+ $\text{D} \times \text{SP}$	-4385.12	30.44	8	$\text{SP} + \text{D} \times \text{SP}$
				$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{L} \times \text{SP}$
24) $Y = \text{Core} + \text{SP} + \text{L} \times \text{SP}$	-4412.43	3.12	7	SP
25) $Y = \text{Core} + \text{SP} + \text{S} \times \text{SP}$	-4407.13	8.42	7	$\text{D} + \text{L} \times \text{D} + \text{S} \times \text{SP}$
26) $Y = \text{Core} + \text{SP} + \text{D} \times \text{SP}$	-4393.53	22.02	7	$\text{D} + \text{L} \times \text{D} + \text{SP} + \text{D} \times \text{SP}$

				SP
27) $Y = \text{Core} + \text{SP}$	-4415.55	0.00	6	D + L x D
28) $Y = \text{Core}$	-4414.77	0.79	5	D + L x D

Model Selected

27) Dependent Variable = Core + Spawnfrequency

TABLE C14. Model selection results for the proportion of all fish surviving after a potential skipped spawning event. A logistic model was used (Proc Genmod SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Probability of Survival the Year After Skipping
	All Fish
Time Period	1997/98–1999/00
Sample Size	1136
Number of Subjects	769
Variance-Covariance Matrix	UN

Description of Independent Variables

D = Density in the year after skipping

S = Sex

SP = If fish skipped spawning the year before the initial year

Model	AICc	delta AICc	No. Param.	Nonsignificant Terms
1) $Y = S + SP + D + S \times D + SP \times D + S \times SP + SP \times S \times D$	1159.95	4.27	8	$S + SP + SP \times D + S \times SP + SP \times S \times D$
2) $Y = S + SP + D + S \times D + SP \times D + S \times SP$	1158.06	2.39	7	$S + SP + SP \times D + S \times SP$
3) $Y = S + SP + D + S \times D + SP \times D$	1156.09	0.41	6	$S + SP + SP \times D$

4) $Y = S + SP + D + S \times D + S \times SP$	1157.66	1.99	6	$S + S \times D + S \times SP$	
5) $Y = S + SP + D + SP \times D + S \times SP$	1160.24	4.57	6	$SP + SP \times D + S \times SP$	
6) $Y = S + SP + D + S \times SP$	1158.50	2.83	5	$S \times SP$	
7) $Y = S + SP + D + SP \times D$	1158.24	2.57	5	$SP + SP \times D$	
8) $Y = S + SP + D + S \times D$	1155.68	0.00	5	$S + S \times D$	
9) $Y = S + SP + D$	1156.51	0.83	4		0
10) $Y = S + SP + S \times SP$	1189.55	33.88	4	$S \times SP$	
11) $Y = S + SP$	1187.93	32.26	3		0
12) $Y = S + D + S \times D$	1178.54	22.87	4	S	
13) $Y = S + D$	1180.90	25.22	3		0
14) $Y = SP + D + SP \times D$	1165.31	9.63	4	$SP + SP \times D$	
15) $Y = SP + D$	1163.37	7.70	3		0
16) $Y = D$	1205.01	49.34	2		0
17) $Y = SP$	1193.39	37.71	2		0
18) $Y = S$	1211.00	55.32	2		0
19) $Y = \text{Intercept Only}$	1231.38	75.71	1		0

Model Selected

8) Dependent Variable = Sex + Spawnfrequency + Density + Sex x Density

Note: Sex and Sex x Density are insignificant – $P = 0.1591$ and $P = 0.0649$ respectively.

However, this model was used as it is only marginally insignificant.

TABLE C15. Model selection results for the proportion of first-time spawners surviving after a potential skipped spawning event in their second year of reproduction. A logistic model was used (Proc Genmod SAS (SAS Institute 2001)).

Dependent Variable = Y	Probability of Survival the Year After Skipping			
	First-Time Spawners			
Time Period	1997/98–1999/00			
Sample Size	643			
Number of Subjects	643			
Variance-Covariance Matrix	N/A (fish only mature once)			
Description of Independent Variables				
D = Density in the year after skipping				
S = Sex				
SP = If the fish skipped spawning the year before the initial year				
		delta	No.	
Model	AICc	AICc	Param.	Nonsignificant Terms
1) $Y = S + SP + D + S \times D +$ $SP \times D + S \times SP + SP \times S \times D$	523.11	4.10	8	$S + SP + SP \times D + S \times$ $SP + SP \times S \times D$
2) $Y = S + SP + D + S \times D +$ $SP \times D + S \times SP$	521.64	2.64	7	$S + SP + SP \times D + S \times$ SP
3) $Y = S + SP + D + S \times D +$ $SP \times D$	519.76	0.76	6	$S + SP + SP \times D$

4) $Y = S + SP + D + S \times D + S \times SP$	520.82	1.82	6	S+ S x SP	
5) $Y = S + SP + D + SP \times D + S \times SP$	524.56	5.56	6	SP + SP x D + S x SP	
6) $Y = S + SP + D + S \times SP$	522.89	3.89	5	S x SP	
7) $Y = S + SP + D + SP \times D$	522.85	3.84	5	SP + SP x D	
8) $Y = S + SP + D + S \times D$	519.00	0.00	5	S	
9) $Y = S + SP + D$	521.12	2.12	4		0
10) $Y = S + SP + S \times SP$	531.35	12.35	4	S x SP	
11) $Y = S + SP$	529.69	10.68	3		0
12) $Y = S + D + S \times D$	522.50	3.50	4	S	
13) $Y = S + D$	524.43	5.43	3		0
14) $Y = SP + D + SP \times D$	536.85	17.85	4	SP + SP x D	
15) $Y = SP + D$	535.19	16.18	3		0
16) $Y = D$	543.43	24.42	2		0
17) $Y = SP$	542.88	23.87	2		0
18) $Y = S$	532.87	13.87	2	S	
19) $Y = \text{Intercept Only}$	550.96	31.96	1	Intercept Only	

Model Selected

8) Dependent Variable = Sex + Spawnfrequency + Density + Sex x Density

Note: Sex is insignificant – $P = 0.1548$.

TABLE C16. Model selection results for the proportion of fish skipping spawning events. A logistic model was used (Proc Genmod SAS (SAS Institute 2001)). Repeated measures variance-covariance matrices are described above.

Dependent Variable = Y	Probability of Skipping Spawning in Year			
	All Fish			
Time Period	1995–1999			
Sample Size	6777			
Number of Subjects	2467			
Variance-Covariance Matrix	UN			
Description of Independent Variables				
D = Density in the Year Skipped				
S = Sex				
		delta	No.	
Model – with D	AICc	AICc	Param.	Nonsignificant Terms
1) $Y = S + D + S \times D$	5577.69	0.00	4	S x D
2) $Y = S + D$	5577.93	0.24	3	0
3) $Y = D$	5669.89	92.20	2	0
4) $Y = S$	5764.09	186.40	2	0
5) $Y = \text{Intercept Only}$	5866.48	288.79	1	0
Model with D-squared	AICc	delta	No.	Nonsignificant Terms

		AICc	Param.	
6) $Y = S + D^2 + S \times D^2$	5555.34	0.11	4	S x D
7) $Y = S + D^2$	5555.23	0.00	3	0
8) $Y = D^2$	5764.09	208.86	2	0
9) $Y = S$	5647.58	92.35	2	0
10) $Y = \text{Intercept Only}$	5866.48	311.24	1	0

Model Selected

7) Dependent Variable = Sex + Density²

TABLE C17. Model selection results for the proportion of first-time spawners skipping spawning events in their second year of reproduction. A logistic model was used (Proc Genmod SAS (SAS Institute 2001)).

Dependent Variable = Y	Probability of Skipping Spawning in Year			
	First Timers			
Time Period	1996–2000			
Sample Size	1604			
Number of Subjects	1604			
Variance-Covariance Matrix	N/A (fish only mature once)			
Description of Independent Variables				
D = Density in the Year Skipped				
S = Sex				
Model – with D	AICc	delta	No. Param.	Nonsignificant Terms
1) $Y = S + D + S \times D$	1674.85	0.00	4	S
2) $Y = S + D$	1679.45	4.60	3	0
3) $Y = D$	1725.62	50.78	2	0
4) $Y = S$	1740.57	65.73	2	0
5) $Y = \text{Intercept Only}$	1794.90	120.06	1	0
Model with D-squared	AICc	delta	No.	Nonsignificant Terms

		AICc	Param.	
6) $Y = S + D^2 + S \times D^2$	1664.18	0.00	4	S
7) $Y = S + D^2$	1669.35	5.18	3	0
8) $Y = D^2$	1725.62	61.44	2	0
9) $Y = S$	1730.87	66.70	2	0
10) $Y = \text{Intercept Only}$	1794.90	130.73	1	0

Model Selected

6) Dependent Variable = Sex + Density² + Sex x Density²

Note: Sex is insignificant – $P = 0.8116$

TABLE C18. Model selection results for the size-at-maturation. A generalized linear model was used (Proc GLM SAS (SAS Institute 2001)).

Dependent Variable = Y	Size-at-Maturation			
	Fork Length			
Time Period	1995–2002			
Sample Size	3111			
Number of Subjects	3111			
Variance-Covariance Matrix	N/A (fish only mature once)			
Description of Independent Variables				
D = Density in the year				
S = Sex				
		delta	No.	
Model – with D	AICc	AICc	Param.	Nonsignificant Terms
1) $Y = S + D + S \times D$	29851.36	0.00	4	0
2) $Y = S + D$	29909.39	58.03	3	D
3) $Y = D$	31521.77	1670.41	2	D
4) $Y = S$	29907.38	56.02	2	0
5) $Y = \text{Intercept Only}$	31523.52	1672.16	1	0
		delta	No.	
Model with D-squared	AICc	AICc	Param.	Nonsignificant Terms

6) $Y = S + D^2 + S \times D^2$	29857.26	0.00	4		0
7) $Y = S + D^2$	29914.77	57.51	3	D	
8) $Y = D^2$	31523.44	1666.18	2	D	
9) $Y = S$	29907.38	50.12	2		0
10) $Y = \text{Intercept Only}$	31523.52	1666.25	1		0

Model Selected

1) Dependent Variable = Sex + Density + Sex x Density

TABLE C19. Model selection results for the age-at-maturation. A generalized linear model was used (Proc GLM SAS (SAS Institute 2001)).

Dependent Variable = Y	Age-at-Maturation			
	Age			
Time Period	1995–2002			
Sample Size	305			
Number of Subjects	305			
Variance-Covariance Matrix	N/A (fish only mature once)			
Description of Independent Variables				
D = Density in the year				
S = Sex				
		delta	No.	
Model – with D	AICc	AICc	Param.	Nonsignificant Terms
1) $Y = S + D + S \times D$	557.34	0.00	4	S
2) $Y = S + D$	559.75	2.41	3	0
3) $Y = D$	584.94	27.60	2	0
4) $Y = S$	604.67	47.33	2	0
5) $Y = \text{Intercept Only}$	622.67	65.33	1	0
		delta	No.	
Model with D-squared	AICc	AICc	Param.	Nonsignificant Terms

6) $Y = S + D^2 + S \times D^2$	553.07	0.00	4	S	
7) $Y = S + D^2$	555.76	2.68	3		0
8) $Y = D^2$	582.12	29.05	2		0
9) $Y = S$	604.67	51.59	2		0
10) $Y = \text{Intercept Only}$	622.67	69.59	1		0

Model Selected

6) Dependent Variable = Sex + Density² + Sex x Density²

Note: Sex is insignificant – $P = 0.7657$

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Appendix D. Multinomial logistic age-at-maturation methods and results.

Age-at-maturation

To analyze the relationship between age-at-maturation and density, a cumulative logistic regression was used, which utilizes a multinomial distribution instead of a binomial distribution in the analysis. This was carried out in Proc Genmod in SAS (SAS Institute 2001). This method fits the cumulative probability of maturing. For example, in this case the probability of maturing at age-6, at age-6 or -7, and at age-6 to -8. After age-8 all fish are assumed to be mature. This analysis is used when there are more than two possible outcomes as would occur when a binomial distribution is utilized. However, the outcome must be an ordinal variable, i.e., $7 > 6$. This method of analysis was used because age-at-maturity is an ordinal variable and is therefore not normally distributed. In this case, density was squared to produce a better fit (Table D1). See [Appendix C](#) for description of model selection methods. Repeated measures were not a concern in this analysis as fish only mature once. For visualization purposes, the results a linear model was also fit to the age-at-maturation data, however, the results of this analysis were also included in Fig. 4.

TABLE D1. Model selection results for the age-at-maturation. A cumulative logistic regression with a multinomial distribution was used (Proc Genmod SAS [SAS Institute 2001]).

Dependent Variable = Y	Age-at-Maturation			
	Age			
Time period	1995–2002			
Sample size	305			
Number of subjects	305			
Variance-covariance matrix	N/A (fish only mature once)			
Description of independent variables				
D = Density in the year				
S = Sex				
Model – with D	AICc	delta AICc	No. Param.	Nonsignificant terms
1) $Y = S + D + S \times D$	546.24	4.44	4	S + S x D
2) $Y = S + D$	541.80	0.00	3	0
3) $Y = D$	571.73	29.92	2	0
4) $Y = S$	589.91	48.11	2	0
5) $Y = \text{Intercept Only}$	611.32	69.52	1	0
Model with D-squared	AICc	delta AICc	No. Param.	Nonsignificant terms
6) $Y = S + D^2 + S \times D^2$	542.29	4.11	4	0
7) $Y = S + D^2$	538.18	0.00	3	0
8) $Y = D^2$	569.24	31.06	2	0
9) $Y = S$	589.91	51.73	2	0

10) Y = Intercept Only	611.32	73.14	1	0
Model Selected				
7) Y = Sex + Density ²				

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SAS Institute. 2001. Online Document, Version 8.2. SAS Institute, Cary, North Carolina, USA.

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Appendix E. Residual plot from analysis of growth in mass.

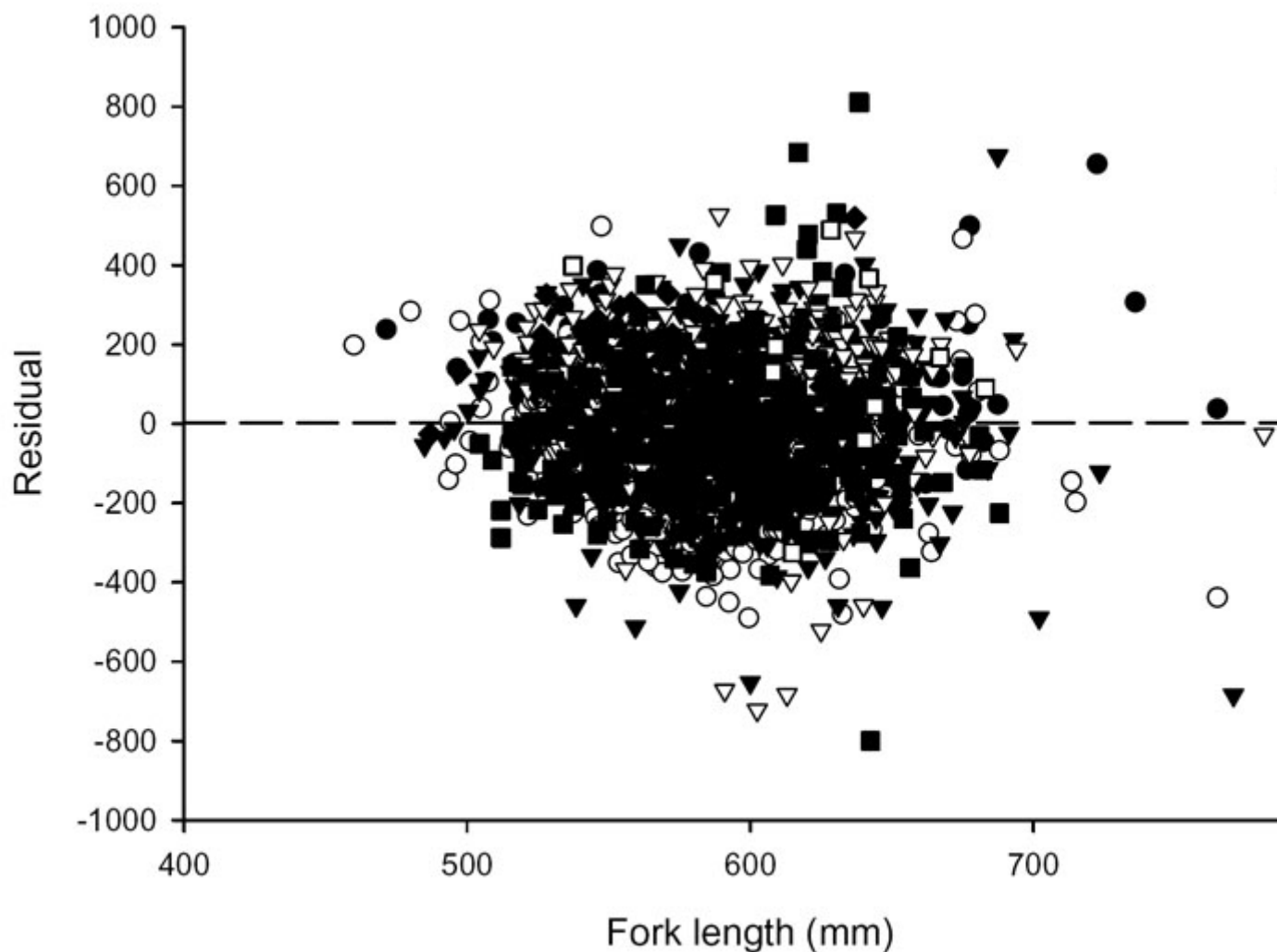


FIG. E1. The distribution of residuals from the analysis of annual growth in upstream weight for adult bull trout in relation to initial length. Proc Mixed (SAS Institute 2001) was used. There were 1467 individuals in this analysis over the period of 1995 to 2001.

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Appendix F. Natural selection analyses results.

Evolution

TABLE F1. The results of the natural selection analysis for Lower Kananaskis Lake from 1995–1996 to 1999–2000. Logistic regression results for all fish together, and only first-time spawners were used (Proc Genmod SAS) (SAS Institute 2001) to examine directional selection and quadratic selection. The opportunity for selection (*I*) (the variance in relative fitness) is also presented. SE = standard error.

Initial Year	Directional Selection			Quadratic Selection			<i>I</i>	Sar Si
	coefficient	SE	<i>P</i>	coefficient	SE	<i>P</i>		
<i>All Fish</i>								
1995	-0.51	0.15	0.0007	0.05	0.13	0.698	0.16	3.
1996	-0.74	0.13	<0.0001	-0.08	0.08	0.339	0.11	6.
1997	-0.22	0.09	0.0115	-0.13	0.05	0.016	0.19	9.
1998	-0.67	0.09	<0.0001	-0.18	0.06	0.002	0.16	12.
1999	-0.33	0.07	<0.0001	-0.08	0.05	0.077	0.45	11.
<i>First-Time Spawners</i>								
1995	-0.50	0.28	0.0712	0.01	0.30	0.973	0.12	2.
1996	-0.69	0.25	0.0055	-0.25	0.19	0.177	0.08	3.
1997	-0.33	0.13	0.0082	0.04	0.11	0.725	0.33	3.
1998	0.01	0.18	0.9712	-0.31	0.11	0.004	0.08	5.
1999	-0.41	0.11	0.0002	-0.13	0.10	0.191	0.55	4.

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SAS Institute. 2001. Online Document, Version 8.2. SAS Institute, Cary, North Carolina, USA.

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