MATURITY, FECUNDITY, GROWTH, AND SUSTAINED YIELD OF COASTAL CUTTHROAT TROUT AT FLORENCE LAKE, SOUTHEAST ALASKA

A

THESIS

Presented to the Faculty
Of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the degree of

MASTER OF SCIENCE

By

Matthew Birch Foster, B. S.

Juneau, Alaska

August 2003

MATURITY, FECUNDITY, GROWTH, AND SUSTAINED YIELD OF COASTAL CUTTHROAT TROUT AT FLORENCE LAKE, SOUTHEAST ALASKA

By

Matthew Birch Foster

RECOMMENDED:

Advisory Committee Chair

Director, Fisheries Division

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

August 18, 2003

Date

ABSTRACT

The resident coastal cutthroat trout *Oncorhynchus clarki clarki* population in Florence Lake, Southeast Alaska was sampled from July through October, 1997 to assess its maturity, fecundity, growth and sustained yield. Maturing female cutthroat have significant gonad development between mid September and late October. A gonadosomatic index threshold was established for female cutthroat trout. A logistic model for maturity estimated asymptotic percentages by age and length: 92% and 100% for males and 86% and 80% for females, indicating presence of skip spawning. Male cutthroat trout matured earlier and at smaller length than females, but females matured more rapidly. An allometric model fitted fecundity data well. Schnute's growth model indicated that growth was relatively slow. An 11-inch (279 mm) minimum size limit allows a high proportion of trout at Florence Lake to spawn at least once. Age-based and length-based per recruit analyses performed comparably and established sustainable fishing mortality estimates.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF TABLES

LIST OF APPENDICES

ACKNOWLEDGMENTS

I would like to gratefully acknowledge my major professor, Dr. Terrance J. Quinn II, who afforded his wisdom, problem solving, and virtue of unwearied instruction in the realization of the study. In addition, I would like to thank my committee members of Dr. Robert P. Marshall, Dr. Thomas C. Shirley, and Dr. William W. Smoker for their support and patience.

I would also like to recognize The Alaska Fish and Wildlife Cooperative Unit and the Alaska Department of Fish and Game, Division of Sport Fish for funding this project. The author is indebted to ADF&G's Art Schmidt and Rocky Holmes for providing the initial support in securing the funding for this project and Dr. James R. Reynolds for his continuous backing through the Co-op unit. The assistance provided by the ADF&G Region I trout research staff was immeasurable. Roger Harding, Doug Jones, Kurt Kondzela, and Ken Koolmo contributed their vast knowledge of cutthroat trout and technical resources to the development of this study. ADF&G volunteers Dan Pieroni and Mike Widman, lended their fish capturing expertise to the success of the pilot studies. Randy Ericksen (ADF&G Haines) and Kris Munk (ADF&G Tag and Otolith Processing Lab) imparted valuable information on aging criteria and techniques.

CHAPTER 1: INTRODUCTION

Historically, cutthroat trout (*Oncorhynchus clarki*) was the most wide-ranging salmonid in North America (Behnke 1992). Coastal cutthroat trout (*O. c. clarki*) is the most extensively distributed and abundant of the four major subspecies of cutthroat trout (Behnke 1992). Coastal cutthroat trout is the only subspecies that exhibits anadromy, and genetic analysis suggests that all other cutthroat subspecies were derived from them (Behnke 1997). The coastal subspecies occur throughout the Pacific coast rain forest belt (Trotter 1987) from Northern California to Prince William Sound in Alaska, with the anadromous, potamodromous, and resident forms frequently coexisting. Northcote (1997) believes that coastal cutthroat trout have the most complex and diverse life history and migrations of any Pacific salmon, trout or steelhead.

Coastal cutthroat trout is the only cutthroat subspecies in Alaska, the most common trout species in Southeast Alaska (Schmidt 1997), and the source of an important recreational fishery. Under a climate of increasing freshwater fishing effort and fishing restrictions, cutthroat trout harvests have declined from about 23,000 fish in 1977, to 15,000 in 1986, to 6,000 in 1994, and to 5,000 in 1999 (Alaska Department of Fish and Game 2001). Whether this trend signals a decline in cutthroat trout abundance, an increasing preference for releasing captured fish (Yanusz 1997), or both, is not known. Regardless, cutthroat populations are thought to be more vulnerable to angling pressure than any other trout (Thurow et al. 1988; Wright 1992), and appear to be highly vulnerable to the effects of logging activities (Behnke 1992). These factors suggest that the health of the Southeast Alaska cutthroat trout populations may be diminished and the regulations governing their catch and harvest should be evaluated.

The Alaska Department of Fish and Game (ADF&G) initiated a cutthroat trout research program in 1988 as a result of a nearly 50% decline in cutthroat harvest in a 14-year period (Harding 1994). Research was accelerated at Turner Lake when it was evaluated as a possible stocking site for five to ten million juvenile sockeye to enhance the Taku Inlet sockeye gillnet harvest and at Florence Lake (Figure 1.1), whose watershed was scheduled for clearcut logging in 1991 (Jones et al. 1989). These projects were designed to provide baseline information needed to sustain and manage the cutthroat trout in these important fly-in systems (Jones et al. 1990). As a result of ADF&G cutthroat trout and steelhead studies in Southeast Alaska, published literature investigations, and an extensive public review process, new trout regulations were adopted in 1994 (Table 1.1). Harvest regulations were rather lenient prior to statehood in 1959 but have steadily become more conservative.

The regulations implemented in 1994 attempt to control for a variety of angling situations through the unification of bag limits, size limits, and bait restrictions. The daily bag limit was decreased from five to two cutthroat or rainbow trout, in combination. This reduction is significant, but a bag limit by itself is not an effective regulatory device because it does not control the harvest of every fish caught like size

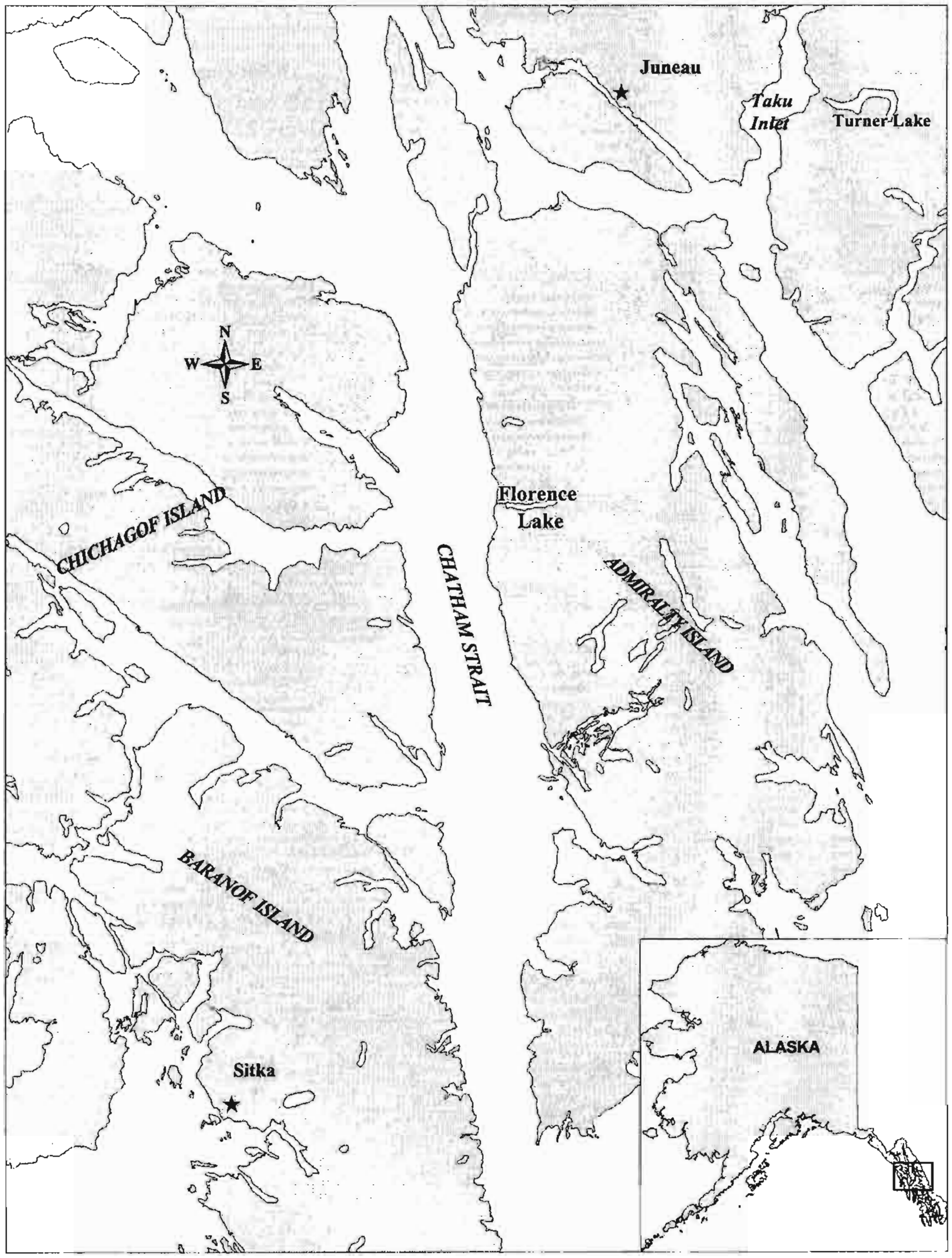


Figure 1.1. Location of Florence Lake, Southeast Alaska.

Table 1.1. History of general regulations affecting trout fisheries in Southeast Alaska (Harding 1994; ADF&G 2003). Beginning in 1994, exceptions to these minimum size limits have been made for a small number of lakes to meet special management goals (Table 1.2).

Years	Regulations
1940's-1959	Twenty trout, grayling, and char daily, three of which may be over 20 inches (508 mm).
1960-1974	Fifteen trout, grayling, and char daily, three of which may be over 20 inches.
1975-1978	Ten trout, grayling, and char daily, two of which may be over 20 inches; possession limit of two bag limits.
1979-1982	Four cutthroat and rainbow trout daily, one of which may be over 16 inches (406 mm); possession limit of one daily bag limit. Steelhead considered separately.
1983-1993	Five cutthroat, rainbow, and steelhead in combination, one of which may be over 16 inches; possession limit of two daily bag limits with two over 16 inches.
1994-1999	Two cutthroat and rainbow trout in combination with a minimum size limit of 12 inches (305 mm) and a maximum size limit of 22 inches (559 mm); possession limit of one daily bag limit. Use of bait prohibited in freshwater from November 16 through September 14. Steelhead considered separately.
2000-present	Two cutthroat and rainbow trout in combination with a minimum size limit of 11 inches (279 mm) and a maximum size limit of 22 inches; possession limit of one daily bag limit. Use of bait prohibited in freshwater from November 16 through September 14. Steelhead considered separately.

limits do (Wright 1992). A skillfully adjusted size limit is the best single regulation preventing anglers from excessive harvest (Hunt 1970). The 12-inch (305 mm) minimum size limit imposed in Southeast Alaska in 1994 attempts to achieve two primary objectives: (1) safeguard steelhead smolt so they will not be harvested before migrating to sea, and (2) protect a "high percentage" of all cutthroat trout until they can spawn at least once (Schmidt 1997). The 22-inch (559 mm) maximum size limit has the purpose of protecting large adult steelhead spawners up to their minimum size limit of 36 inches (914 mm). For size limits to work, hooking mortality must be minimized. Hooking mortality studies have found cutthroat trout to be especially susceptible to bait fishing (Hunsaker II and Marnell 1970; Taylor 1992; Pauley and Thomas 1993). In all of these studies, baited hooks incurred approximately 50% mortality when an angler is catching and releasing cutthroat, while non-baited gear types ranged from 2.7–23.8%. Therefore, bait fishing was prohibited in freshwater for ten months out of the year. These guidelines regulated the "general-use" lakes in Southeast Alaska (Table 1.1).

There are exceptions to the general regulations that govern high-use, trophy, stocked, small, and special lakes (Table 1.2). The exceptions consider specific lake situations but highlight the position that regulations crafted for general use may be inadequate, because different trout stocks (large rapid-growing and small slow-growing) have different sizes at maturity (Dahl 1917). Jonsson et al. (1984) theorized that cutthroat trout mature at an age which maximizes the reproductive potential over their lifespan, and that fish can regulate their maturation age, non-genetically, to growth rate variations. These growth

Table 1.2. A summary of special regulations affecting the trout fisheries in Southeast Alaska (ADF&G 2003).

Lake Type	Regulations
High-use	For 28 lakes with developed access and/or intensive fisheries. A minimum size limit of 14 inches (356 mm) and a maximum size limit of 22 inches (559 mm). Use of bait prohibited year-round.
Trophy	For 13 lakes which have all produced trophy (3 lb.) cutthroat trout. A minimum size limit of 25 inches (635 mm). Use of bait prohibited year-round.
Stocked	Lakes stocked on a regular basis. Five trout daily; possession limit of one daily bag limit. No minimum size limit. Use of bait allowed year-round.
Small	For 6 small lakes with few, if any, cutthroat trout of legal harvest size. A minimum size limit of 9 inches (229 mm).
Special	*Florence lake*: Five cutthroat trout daily with no size limit; possession of 2 daily bag limits. Use of bait allowed year-round. This is due to a large population and minimal fishing effort. *Turner Lake*: Catch and release fishery only. Use of bait prohibited year-round. This is due to population abundance concerns.

variations are enormously influenced by environmental factors affecting metabolism (Behnke 1992). Growing season and water temperature likely play a role in growth (Carlander 1966) and are affected by numerous variables like latitude, elevation and climate. There is increasing realization, as evidenced by the special regulations, that parameters controlling trout harvest in a lake should incorporate factors that describe the population's productivity as well as expected fishing pressure.

When the Southeast Alaska general trout regulations were amended in 1994, minimal age- and length-at-maturity information existed on cutthroat trout in Southeast Alaska, especially for non sea-run populations. Such information will allow fishery managers with the ADF&G to better draft angling regulations to the Alaska Board of Fisheries to ensure preservation of the trout populations and quality fishing in Alaska's trout lakes. In addition, long term information on changes in age at maturity can be an indicator of changes in size structure and stress of a fish population (Trippel 1995).

Precise discrimination between mature and immature fish is one of the essential research questions in the study of ecology and life history of a species (Ishida et al. 1961). Furthermore, age- and length-at-maturity information provides knowledge critical to the creation of regulations that will sustain balanced trout populations (Avery 1985). The State of Alaska Constitution is the only state constitution that explicitly mentions fisheries and it requires that they be managed on a sustained yield basis. The concept of managing Southeast Alaska's trout fishery using sustained yield theory can be included more explicitly into research and management programs. Quinn and Szarzi (1993) proposed an age-based model to determine sustained yield in recreational fisheries. Such a detailed, age-based population model has not been constructed for a native trout population in Southeast Alaska.

There are two main objectives of this study: (1) to gather and analyze maturity, fecundity, and growth data from Florence Lake cutthroat trout, and (2) to evaluate the sensitivity of the population to different minimum size limits (MSL's). Florence Lake was selected for this study due to the wealth of information collected during a mark-recapture experiment and weir study in the inlet creeks conducted between 1991 and 1994.

In chapter two, I report results obtained from the field studies conducted during the summer and fall of 1997 to estimate age- and length-at-maturity, and fecundity. Models of growth are also presented. In chapter three, I study the effect of different sized-based regulations on the cutthroat trout population of Florence Lake. This was done using the basic framework provided by Quinn and Szarzi (1993) for determining sustained yield, utilizing the results obtained in chapter two and estimates of natural mortality and selectivity. Due to the difficulty in aging a slow-growing, relatively long-lived trout population such the one in Florence Lake, an alternative length-based model (Quinn et al. 1998) is constructed and compared to that of the age-based method.

CHAPTER 2: MATURITY, FECUNDITY, AND GROWTH

INTRODUCTION

Florence Lake is approximately 50 km southwest of Juneau on the west side of Admiralty Island at longitude 134° 04′ W, latitude 58° 03′ N (Figure 1.1) with a surface elevation of 45 meters. It is a narrow lake about 7.2 km long and less than 1.0 km wide with a surface area of 347.73 hectares (B. Frenette, ADF&G, personal communication) and a maximum depth of 27 meters (Harding 1999), but a majority of the lake is less than 18 meters (Figure 2.1). The outlet creek flows approximately 1 km into Chatham Strait and due to a barrier falls, the cutthroat trout population is solely lake-dwelling, except for a few cutthroat that may descend the falls and contribute to a sea-run population (R. Harding, ADF&G, personal communication).

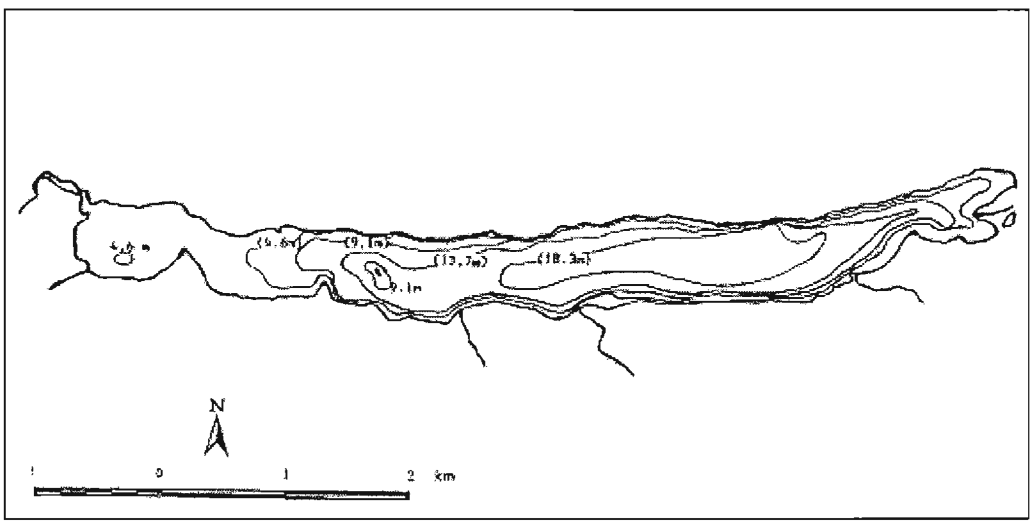


Figure 2.1. Bathymetric map of Florence Lake, Southeast Alaska (Jones et al. 1989).

The fish species present in Florence Lake are cutthroat trout, Dolly Varden *Salvelinus malma*, kokanee *Oncorhynchus nerka* (landlocked form of sockeye salmon), prickly sculpin *Cottus asper*, and threespine stickleback *Gasterosteus aculeatus*. From 1967 to 1995, three of the 88 trophy cutthroat trout registered with ADF&G in Southeast Alaska were from Florence Lake, the largest weighing 4 pounds and 10 ounces (J. Andel, ADF&G, personal communication). With two U.S. Forest Service cabins, Florence Lake was a very popular angling location until 1991 when logging operations began to strip the watershed of almost all of its marketable timber. Since that time, angling interest in Florence Lake has decreased (D. Jones, ADF&G, personal communication) yet, a 1994 survey of registered U.S. Forest Service cabin users indicated the lake still received considerable fishing effort relative to other Southeast lakes (Jones 1995). The effect of logging the Florence Lake watershed on the cutthroat trout population is unclear at this time. However, a study on a small coastal tributary in Oregon showed that clearcutting without buffers (the practice at Florence Lake) decreased the abundance of juvenile coastal cutthroat trout to one third its size before logging, and reduced the population for 25 years (Hooton 1997).

Like all trout, cutthroat are iteroparous; i.e., they have the capacity to spawn multiple times. In general, potamodromous coastal cutthroat trout in lakes spawn anytime from February to June (Trotter 1989). In Southeast Alaska, cutthroat trout generally spawn in April or May (Trotter 1987) or late March through May (Jones and Seifert 1997), but this timing is dependent upon the locale (Trotter 1997). Cutthroat trout, like all trout native to western North America, evolved to spawn with the increasing water temperatures of the springtime (Behnke 1992). Typically this occurs when the water temperatures are about 5–6°C (Trotter 1989). Weir data from Florence Lake inlet creeks, from 1992 and 1993 (Harding 1994), indicated spawning occurs between late April and May as the lake surface water temperature increased from 4.5° C in mid April to 6.0° C at the end of April.

The spawning behavior of cutthroat trout is similar to that of other trout and the Pacific salmon (Trotter 1997). The female constructs a redd in the gravel in streams and deposits her eggs while the male fertilizes the eggs with his milt (Pauley et al. 1989). At Petersburg Creek, Alaska, individual cutthroat trout spawning takes place over a period of 4–5 days; the actual egg deposition and fertilization occur during the night (0000 to 0500), the fish return to Petersburg Lake during the daylight hours (Jones 1976). In general, cutthroat trout spawning transpires during the day or night, and both males and females may spawn with multiple members of the other sex (Morrow 1980). A majority of the cutthroat trout spawning at Florence Lake probably occurs in three major inlet creeks (Jones 1981), but the outlet creek, above the falls, also contains suitable spawning substrate (R. Harding, ADF&G, personal communication).

After about 6–7 weeks of incubation, the eggs hatch with the alevin about 15 mm in length (Morrow 1980), and in 1–2 weeks, the fry emerge from the gravel measuring about 25 mm (Trotter 1997). Emergence occurs around July at Florence Lake (D. Jones, ADF&G, personal communication) and cutthroat trout normally rear in small streams for the first two years of life (Schmidt 1997). During the spring, summer, and fall, relatively high numbers of cutthroat trout young-of-the-year (fry) and juveniles (<2 yr) utilized Sprout Fork, an inlet creek at Margaret Lake, Southeast Alaska (Bryant and McCurdy 1995). Because of limited number and size of inlet creeks at Florence Lake that are ice-free year round, the juvenile cutthroat trout may occupy the lake margins during the winter. During the summer, juvenile cutthroat trout have been observed rearing in very small inlet creeks (one to two feet in width) at Florence Lake (R. Harding, ADF&G, personal communication).

Age and length at maturity of coastal cutthroat trout is poorly documented in the literature. Prior to this study, there has never been a comprehensive examination of age and length at maturity for resident cutthroat trout in Southeast Alaska.

PURPOSE

The purpose of this study was to obtain and analyze maturity, fecundity, and growth information of resident cutthroat trout in Florence Lake via a series of pilot studies from July to September and a main maturity study in October 1997.

OBJECTIVES

1) Observe the development of female cutthroat trout ovaries throughout the summer at Florence Lake to determine a period in the fall, when maturity (spawning the subsequent spring) determination will be definite in Southeast Alaska. Null hypothesis: In the fall, there is not a visible difference between gonads of cutthroat trout at Florence Lake that will spawn next spring and those that will not.
2) Establish a gonadosomatic index of Florence Lake cutthroat trout. Null hypothesis: A quantitative rationale to determine maturity for cutthroat trout females cannot be established.
3) Estimate the proportion of cutthroat trout in Florence Lake that are sexually mature at length and age. Null hypothesis: Age and length at maturity will not differ between the sexes for cutthroat trout in Florence Lake.
4) Estimate fecundity of female cutthroat trout as a function of fork length (mm) in Florence Lake. Null hypothesis: Fecundity does not change with size.
5) Estimate the growth parameters of cutthroat trout in Florence Lake. Null hypothesis: Growth parameters of male and female cutthroat trout are not significantly different.

METHODS

Sample timing and size

Spawning aggregations at Florence Lake during the spring may prevent a random sample from being obtained. Thus, the cutthroat trout maturity samples were collected in the fall before the lake surface froze or wintry weather impeded sampling. Fall was assumed to be an ideal time to sample cutthroat trout for maturity determination, because the fish are believed to be more uniformly distributed than they would be in the spring. In addition, cutthroat trout occupying the northerly part of their range (Southeast Alaska) chiefly utilize winter energy resources for sustenance and significant gonadal development does not occur (Behnke 1992). Therefore, cutthroat trout gonads must be in an advanced stage of development in the fall if they are to spawn the following spring (Behnke 1992).

The initial cutthroat trout maturity study at Florence Lake commenced in July 1997. After spring spawning, pilot studies were conducted in July, August, and September to observe the development of the cutthroat trout gonads over the summer and select an appropriate time in the fall to sample. Cutthroat trout were captured during the pilot studies with large traps baited with salmon eggs and hook and line effort. The purpose of the pilot studies was two-fold; to serve as a maturity sampling time indicator, and to aid in the main study's sample size determination. Sampling was optimized, a priori, to estimate the percentage of mature females (p) in each of the ten (20 mm) categories. Sample sizes were constructed to permit each length class proportion to be estimated within 0.2 of the true proportion with 90% confidence (Thompson 1992).

Data collection

On 27–29 October 1997, the main maturity sampling study was conducted at Florence Lake. Cutthroat trout were captured at seventeen randomly located sites across the lake, with floating and sinking variable mesh gill nets and large hoop traps baited with Betadine-treated salmon eggs. All trout captured were kept unless the sample size prescribed for a certain length class was filled. The decision to keep a fish was based solely on the number of fish already sampled in each 20 mm length increment. While females were desired for the study, attempting to choose fish based upon morphological characteristics would most likely bias this sample toward mature females. The sacrificed fish were measured to the nearest fork and total length (mm), weighed (g), and sexed. In addition, scales and otoliths were extracted and maturity was determined according to Downs et al. (1997). Ovaries were extracted and fixed in a 10% buffered solution of formalin. While maturity was determined for males, unlike the females, the gonads were not extracted and preserved.

Analysis of gonads

The gonads were weighed to the nearest 0.01 grams, strained of the formalin solution, and transferred to a 70% alcohol solution. Ova of the mature females were later enumerated for a measure of fecundity by an ADF&G technician and the diameter of a random sample of 30 ova from each was measured for an estimate of egg size. A compound microscope interfaced with a personal computer utilizing Optimas software was used for the measurements.

Gonadosomatic index

In general, ovary size in fishes increases with stage of development and with fish size (Bunag 1956). Also, Avery (1985) found that the larger the female trout, the higher the percentage body weight was used for egg production. By considering the connection between body weight, ovary weight, and maturity stage of trout, I developed a gonadosomatic index (GSI) (West 1990) for Florence Lake cutthroat trout by dividing ovary weight by fish weight and then plotting it versus length. This index offers a validation of maturity determination based on the amount of gonad development versus the size of the fish.

Aging

Ericksen (1997), in comparison of scales to otoliths for Florence Lake cutthroat trout, found no significant systematic discrepancy between ages acquired from each structure. It is difficult to discern annuli on Florence Lake cutthroat trout scales, but careful examination can yield the correct number of annuli on most of them (Ericksen 1997). A manual for aging the scales of cutthroat trout of Southeast Alaska was authored by Ericksen (1999), with Florence Lake cutthroat utilized as an example, and contains criteria for aging cutthroat trout scales that were developed in his 1997 Master's thesis. Whereas otoliths are often preferred over scales for aging fishes, more research is needed on cutthroat otoliths to define criteria used to age them, as well as to assess the accuracy and precision compared to scales (R. Erickson, ADF&G, personal communication). Therefore, scales were used to estimate the age of the cutthroat trout in this study, following the criteria defined by Ericksen (1999). Between 2 and 4 non-regenerated scales from the 20 to 30 scales collected from each fish in the maturity study were mounted between two glass microscope slides and examined under high magnification (100x) with a compound stereomicroscope. Age was determined in two separate readings to assess reader precision and then ages differing between the two readings were examined for a consensus age. In addition, each scale was digitally captured using Biosonics Optical Pattern Recognition System (OPRS) software and the total number of circuli was enumerated. OPRS was originally designed to measure and enumerate the circuli in the freshwater growth region of a sockeye salmon scale for stock separation discriminant analysis. No true age validation study was conducted to assess the accuracy of the ages, however a qualitative length frequency analysis using the fork lengths of the 12,000+ cutthroat trout sampled during the mark-recapture experiment at Florence Lake from 1991–1994 is compared to the length-age data compiled in this study.

Length and age at maturity

After maturity was determined and aging was performed, the estimated proportion mature for length class x was calculated as:

$$\hat{p}_x = \frac{m_x}{n_x}, \tag{2.1}$$

where m_x is the number of cutthroat trout in length group x that are mature, and n_x is the sampled number of cutthroat trout in the length group. The estimated variance (Thompson 1992) associated with this estimate of the maturity proportion is:

$$\hat{\text{var}}(\hat{p}_x) = \frac{\hat{p}_x(1-\hat{p}_x)}{n_x - 1}. \tag{2.2}$$

Maturity at length was estimated by fitting the data to the common logistic maturity equation (Quinn and Deriso 1999),

$$p_x = \frac{m_\infty}{1 + e^{-\kappa(x-\gamma)}}. \tag{2.3}$$

where p_x is the proportion of cutthroat trout mature at length x. The asymptotic maturity parameter m_∞ is the maximum achievable maturity proportion, κ is the instantaneous rate of fish maturation which characterizes the curve of the logistic function, and γ is the length of the fish at which the inflection point of the curve occurs. Since sample size is fairly large ($n > 100$), the normal approximation of the multinomial distribution was used and a nonlinear weighted least squares optimizing scheme was used in Excel to estimate the parameters. The squared residual for each length class was weighted by the sample size in that category. This method allows the influence of a length category, in optimization, to be based upon number of fish sampled, which is an advantage over common maturity estimation methods such as logit analyis or simple linear regression (Trippel and Harvey 1991). Standard errors of the parameter estimates were estimated using the Hessian method and also validated by constructing a Visual Basic bootstrap resampling procedure in Excel. A similar approach was employed to estimate age at maturity, with the exception that a "plus" group that was used for fish age 9 and older.

Fecundity

Fecundity data were analyzed by simple linear regression. By assuming fecundity to be allometrically related to length (Quinn and Deriso 1999) with multiplicative error (variance increasing with increasing length), fecundity was modeled as

$$\tilde{f}_i = \alpha L_i^{\beta} e^{\varepsilon_i}, \tag{2.4}$$

where L_i is the total length of the fish (mm), α and β are the allometric parameters, and ε_i is an error term with mean zero and constant variance. The parameters α and β were estimated by logarithmically transforming the length and fecundity variables and fitting the linear regression:

$$\ln \tilde{f}_i = \ln \alpha + \beta \ln L_i + \varepsilon_i. \tag{2.5}$$

Standard errors of ln α and β were estimated from the linear regression; the standard error of α was obtained via the delta method (Seber 1982). An additive error structure was also examined and compared to the multiplicative by using nonlinear least squares to fit the untransformed fecundity-at-length data to the model. Standard errors of α and β were estimated using the Hessian method.

Growth

The length and age data from October were used for a growth analysis of Florence Lake cutthroat trout. Growth of males and females was modeled separately using Schnute's (1981) flexible four parameter growth model and examining both additive and multiplicative (natural log transformed length data) error structures. If there was no significant difference in growth parameters between males and females, the data were pooled to increase sample size and decrease the variance of the parameter estimates.

The Schnute growth model is formulated as a general (four parameter) model, with submodels simply consisting of parameter restrictions resulting in historically popular models. Gompertz, von Bertalanffy (LVB), Richards, logistic, power series: linear and quadratic, and exponential growth can result depending on the model's parameters. The four parameters κ, γ, y_1, and y_2, are based upon biological fundamentals and almost invariably produce statistically stable estimates (Schnute 1981). Schnute's model is based upon logarithmic or relative rate of change. Parameters κ and γ are connected to the relative rates of growth encountered by fish at different ages and y_1 and y_2 coincide with the mean length at ages τ_1 and τ_2. These ages are designated by the modeler, and I chose them to be the youngest and oldest ages observed in the sample. The four cases of Schnute's model pertaining to whether κ and/or γ are equal to 0 are:

Case 1. $\kappa \neq 0$, $\gamma \neq 0$:

$$Y(t) = \left[y_1^{\gamma} + (y_2^{\gamma} - y_1^{\gamma}) \frac{1 - \exp(-\kappa(t - \tau_1))}{1 - \exp(-\kappa(\tau_2 - \tau_1))} \right]^{1/\gamma}, \tag{2.6}$$

Case 2. $\kappa \neq 0$, $\gamma = 0$:

$$Y(t) = y_1 \exp\left[\ln(\frac{y_2}{y_1}) \frac{1 - \exp(-\kappa(t - \tau_1))}{1 - \exp(-\kappa(\tau_2 - \tau_1))} \right], \tag{2.7}$$

Case 3. $\kappa = 0$, $\gamma \neq 0$:

$$Y(t) = \left[y_1^{\gamma} + (y_2^{\gamma} - y_1^{\gamma}) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{1/\gamma}, \tag{2.8}$$

Case 4. $\kappa = 0$, $\gamma = 0$:

$$Y(t) = y_1 \exp\left[\ln(\frac{y_2}{y_1}) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]. \tag{2.9}$$

Schnute's four cases permit eight different curve types depending on positive and negative values of κ and γ. The popular LVB model corresponds to $\gamma = 1$; thus a case five is added of the form:

Case 5: $\kappa \neq 0$, $\gamma = 1$:

$$Y(t) = y_1 + (y_2 - y_1) \frac{1 - \exp(-\kappa(t - \tau_1))}{1 - \exp(-\kappa(\tau_2 - \tau_1))} . \tag{2.10}$$

The five cases above were fitted to the age and length data with nonlinear least squares, and both additive and multiplicative error structures were considered. Choice of error structure was made by examination of residuals plots. To compare cases, Schnute (1981) presented an F-test procedure,

$$\mathrm{F} = \frac{RSS_y - RSS_x}{f_y - f_x} / \hat{\sigma}_x^2, \tag{2.11}$$

where RSS_y is the residual sum of squares of case y, f_y is the degrees of freedom (n minus # of parameters), and $\hat{\sigma}_x^2$ is equal to RSS_x / f_x, the residual mean square. The null hypothesis that case x does not fit the data better than case y was tested by comparing F to the critical value of the F distribution for a one-sided test with $\alpha = 0.05$. The numerator degrees of freedom is $f_y - f_x$ and the denominator degrees of freedom is equal to f_x. The model chosen was the one with the fewest number of parameters that is still statistically the same as case 1 and complies with the assumptions of the least squares regression method.

RESULTS

Sample timing and size

The monthly pilot studies began on 22 July 1997, with 35 cutthroat trout sampled (25 females), 38 (18 females) on 20–21 August, and 37 (19 females) on 16 September. During the main study in October, 237 fish (140 females) were collected throughout different areas of the lake. There was little visible difference in the gonads of cutthroat trout between July and August. In September, a distinction between those fish that had developed gonads and those that had not was beginning to appear. During the main study in late October, there was a concise difference between the apparent immature and maturing trout. Ovary weight plotted against fork length (FL; mm) illustrates the change in ovary weight through the summer and into the fall (Figure 2.2). Between mid-September and late October, there is evidently an enormous amount of energy employed for gonad development.

The sample size requirement of 137 females in different twenty-millimeter length categories, derived from the pilot study data, was met (with 140 females sampled). The individual sample sizes needed for the length categories were adjusted slightly upward to compensate for the proportions mature being found in the field. This compensation was attributed to the error associated with the pilot study's estimation of the true value and the growth of the fish that occurred between the pilot studies and the main study.

Data collection

The samples were obtained from different depths, areas of the lake, and gear types. Since

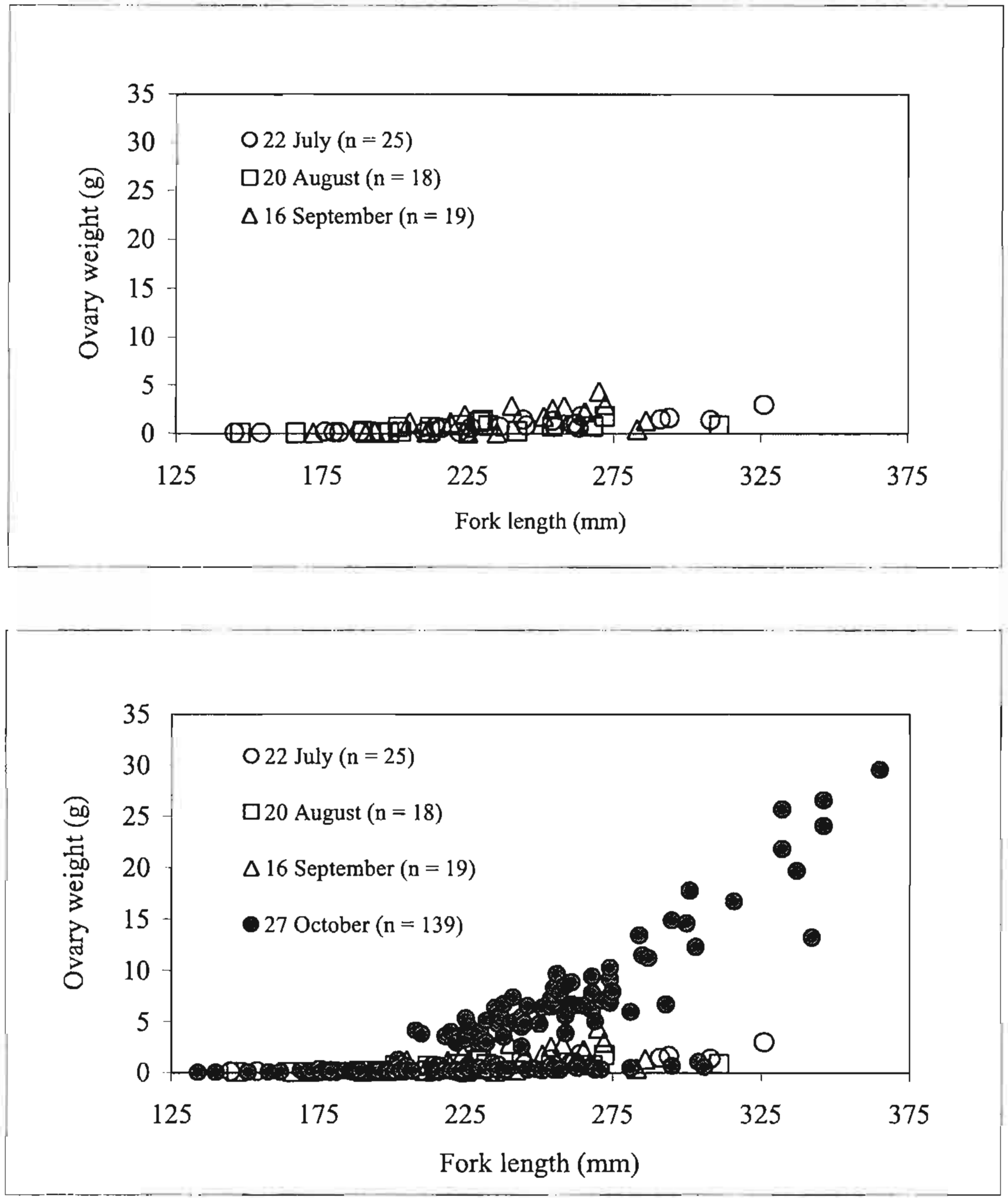


Figure 2.2. Ovary weight versus length of cutthroat trout at Florence Lake, from July to October 1997.

no attempt was made to sample a fish based upon morphological characteristics, the sex ratio estimated for Florence Lake is assumed to be unbiased. The male to female ratio estimated in the main study was 41:59 (n = 237) and in the pilot studies was 44:56 (n = 110). Combining the main and pilot studies produced a male to female ratio of 42:58 (n = 347) with a standard error of 2.6. The uneven sex ratio is roughly equivalent to that found for cutthroat trout in the Mosquito Lake system in Queen Charlotte Islands, British Columbia (40% males) (Leeuw 1987). To test if the sex ratio changes as a function of age or length class, a chi-square test of homogeneity was performed. The null hypothesis of homogeneity was not rejected for both age (P = 0.33) and length class (P = 0.74).

Female cutthroat trout specimens collected ranged from 134 to 365 mm (FL) and males ranged from 141 to 374 mm (FL). Fish weights ranged from 23 to 536 grams (App. Table A.1).

Analysis of gonads

Inspection of the gonads revealed both sex and maturity status of the fish. It was not possible to consistently determine the sex of the cutthroat trout by external morphological characteristics. However, sexual dimorphism was evident for larger fish (> 300 mm), with the males possessing an elongated and hooked upper jaw. Maturity determination was relatively simple. Mature females possessed skein-enclosed orange-colored ova that were visibly egg-like to the naked eye, while immature female ovaries were also usually orange but were considerably smaller in size and contained minute ova. The size range of ovum size from mature individuals contrasted sharply with ovaries from the more developed, but immature fish (Figure 2.3). Mature males had puffy, white developed testes, while the gonads of immature males consisted of miniscule strand-like viscera. Color of the gonads was not important in determining maturity, but was useful in determining sex of the small and immature fish.

Fecundity of mature females ranged from 132 for a 222 mm fish to 707 for a 346 mm fish (App. Table A.1). Of the 70 mature females, 52 were sampled for egg size analysis. Average egg diameter ranged from 2.45 to 4.37 mm and the estimated standard error averaged 0.022 (App. Table A.2). A linear regression of egg diameter on fork length indicated egg diameter to be an increasing function of size (Figure 2.4), although only about half of the variation was explained ($R^2 = 0.468$, $P < 0.005$). Ovary weights ranged from 0.02 to 1.37 grams for immature individuals and 2.58 to 29.57 grams for mature (App. Table A.1).

Residual eggs (eggs not shed when spawned that spring) were found in 14 of the 140 females sampled. Of those 14 fish, 8 were preparing to spawn the next spring and 6 were not. The residual eggs did not have the characteristic orange color, but appeared white and collapsed. The average length of the eight repeating spawners was 258 mm (SE = 17.2) and the average length of the six skip-spawners was 235 mm (SE = 8.9).

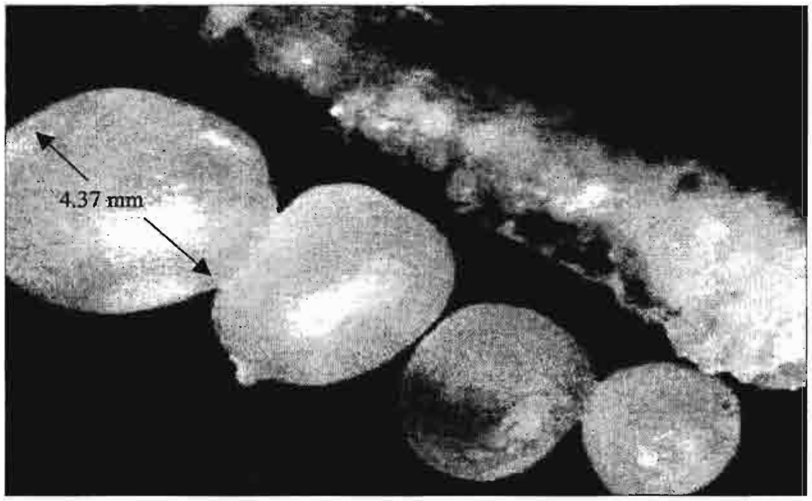


Figure 2.3. The range in size of the ova of mature individuals in comparison to an ovary of a developed, but immature, cutthroat trout at Florence Lake.

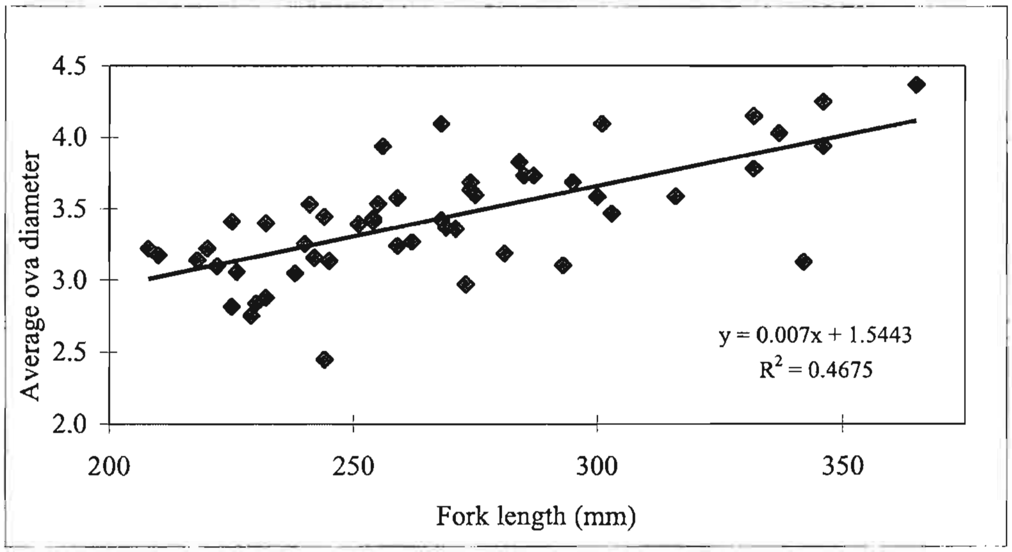


Figure 2.4. Regression of ova diameter on length, for cutthroat trout at Florence Lake.

Gonadosomatic index

The GSI fundamentally agreed with the macroscopic field maturity determination. Little overlap occurred between mature and immature individuals in respect to the clusters that the GSI revealed (Figures 2.5–2.6). GSI's calculated for the female cutthroat trout sampled during July, August, and September, clearly do not quantify maturity status (Figure 2.2). GSI's for immature cutthroat ranged from 0.00065 to 0.016, and for mature cutthroat ranged from 0.018 to 0.069. A frequency plot displaying the GSI's of female cutthroat trout is depicted in Figure 2.6 with the GSI maturity boundary developed in this study indicated by a dotted line (0.018). The GSI plot (Figure 2.5) revealed four possible outliers; points that did not appear to be a strong constituent of either the mature or immature cluster. All of these fish had their weights checked for error by comparing to the length-weight relationship established from this study. Their preserved ovaries were also re-weighed. No errors were found, so the ovaries were visually analyzed again to determine maturity. Re-analysis changed the maturity status for one fish from mature to immature (marked with an arrow in Figure 2.5). This fish had the lowest GSI of the mature fish and did not appear to be in either cluster and, upon reclassification into the immature group, had the highest GSI of the immature fish.

The analysis of the gonads during the pilot and main maturity studies, in addition to the results of the GSI, resulted in the rejection of the null hypothesis that, in the fall, there is not a visible difference between gonads of cutthroat trout at Florence Lake that will spawn next spring and those that will not. Furthermore, the discrimination ability of the

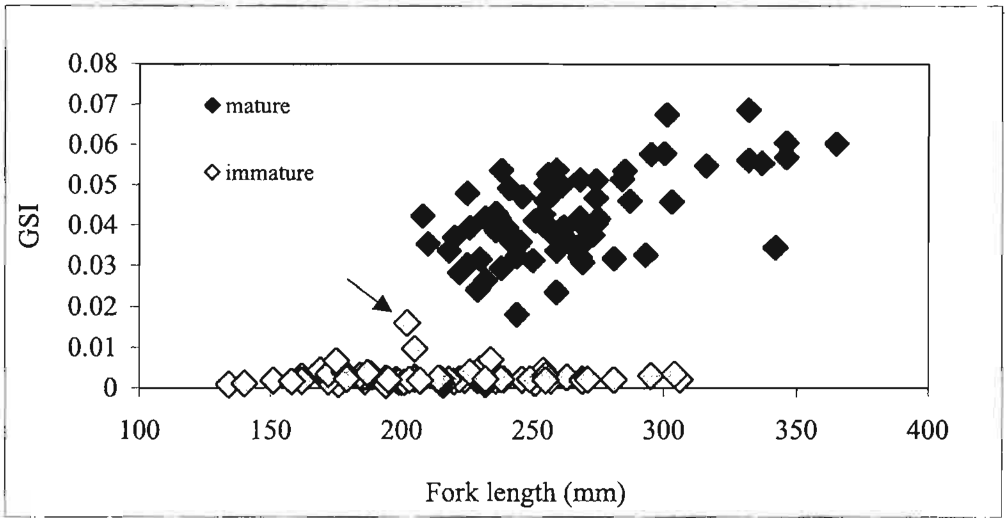


Figure 2.5. Gonadosomatic Index (GSI; ovary weight divided by body weight) for cutthroat trout at Florence Lake, October 1997.

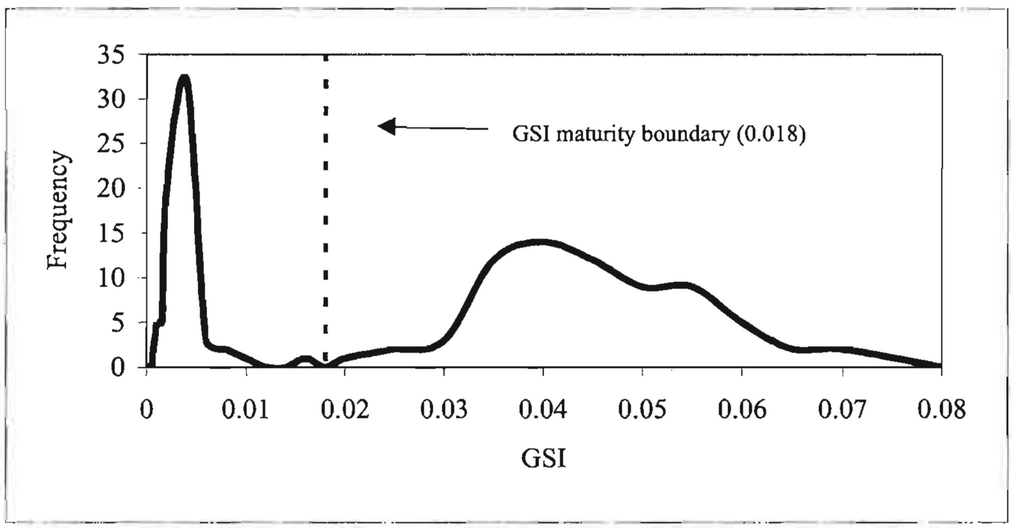


Figure 2.6. Frequency plot of calculated GSI's from mature and immature female cutthroat trout (with GSI maturity boundary indicated) at Florence Lake, October 1997.

GSI leads to rejecting the null hypothesis that a quantitative rationale to determine maturity for cutthroat trout females cannot be established.

Aging

The age estimates for cutthroat trout (134 to 374 mm) ranged from age 3 to age 12. Agreement between the two readings was 64.6%, however, 92.0% of the time, the ages were within one year of each other. A test of symmetry between the two readings (Hoenig et al. 1995) revealed no significant bias between the two readings ($P = 0.742$). Circuli enumerated on the cutthroat scales using Biosonics OPRS ranged from 19 for a 152 mm age 3 fish to 71 for a 342 mm age 12 fish (Figures 2.7 and 2.8). A linear regression of the number of scale circuli on length (mm) had a significant slope ($P < 0.005$) and a R^2 value of 0.66 (Figure 2.7). The number of scale circuli increased with increasing age as well (Figure 2.8).

Qualitative analysis of the length frequencies of the 12,000+ cutthroat trout sampled in the Florence Lake mark-recapture experiment from 1991-1994 (Figure 2.9) suggested the ages estimated were reasonable. In general, only fish over 180 mm fork length were sampled during the mark-recapture experiment, consequently, length frequency peaks can only be inspected above 180 mm. Between 200 mm and 325 mm the length-frequency plot displays 7 peaks (Figure 2.9). Correspondingly, the ages estimated as a part of this maturity study generated 7 age classes between 200 mm and 325 mm. This interpretation

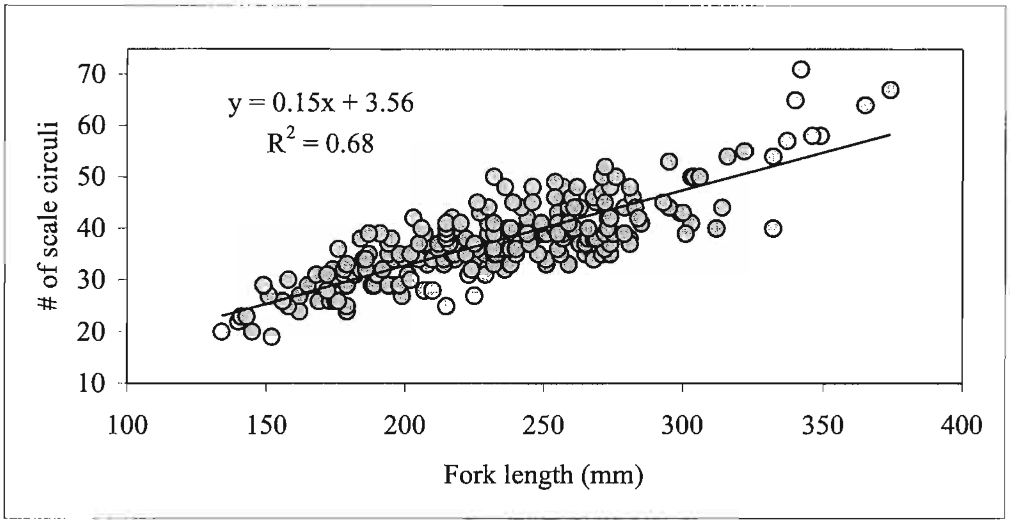


Figure 2.7. Linear regression of the number of scale circuli on fork length for cutthroat trout at Florence Lake. The number of circuli was estimated using OPRS.

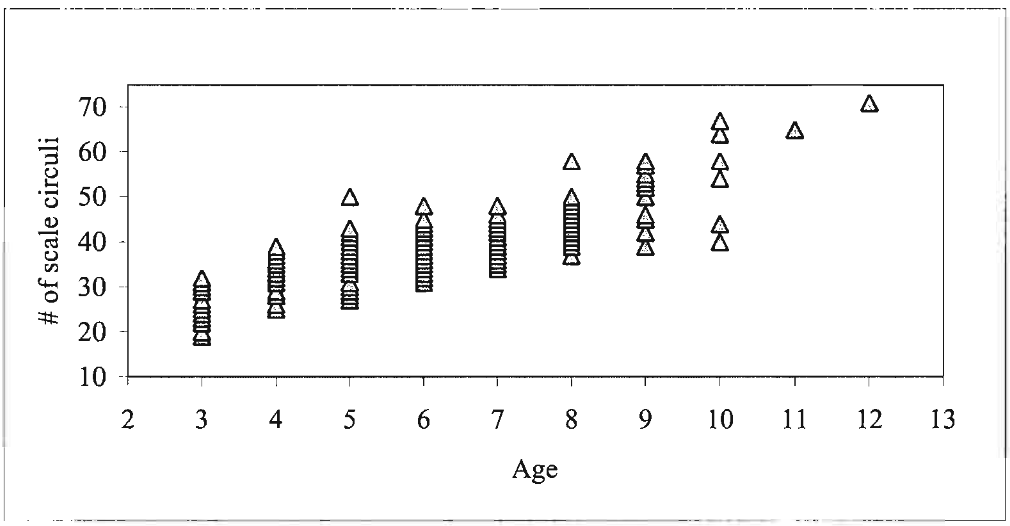


Figure 2.8. Scatterplot displaying the number of scale circuli versus age for cutthroat trou Florence Lake. The number of circuli was estimated using OPRS.

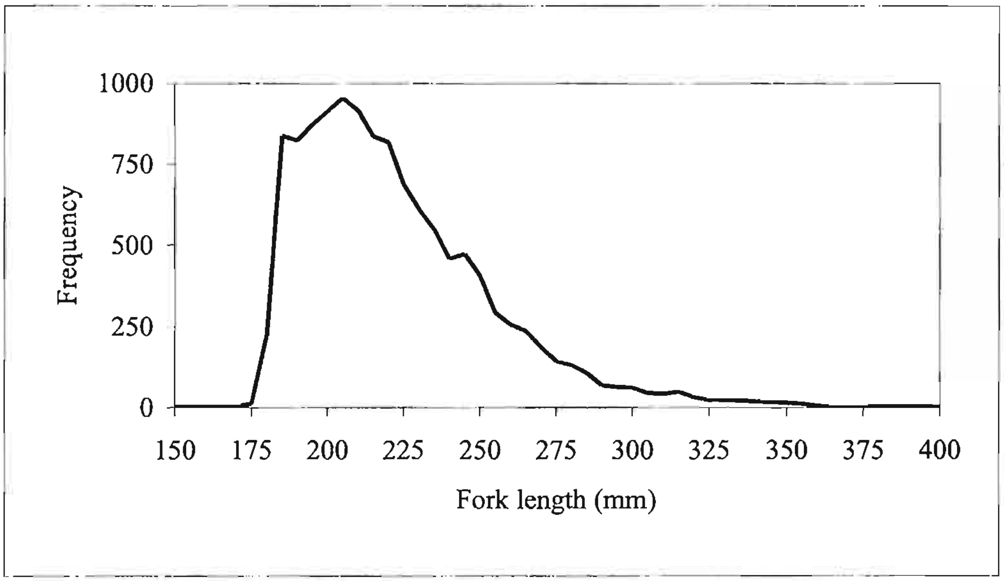


Figure 2.9. Length-frequency plot of the fork lengths (mm) of cutthroat trout sampled in the mark-recapture experiment at Florence Lake from 1991 to 1994.

is arguable however, in part because of the range of years and seasons that the mark-recapture samples were collected.

Length and age at maturity

Maturity was determined based on the cutthroat trout preparing to spawn the next spring. Since the ages were estimated from the fish in October, they would be one year older when they spawn the next year; therefore, in describing age at maturity it is necessary to add one year to age estimates for proper designation. The youngest mature male was age four and the youngest mature female was age 6. Both males and females demonstrated consecutive increases in maturity with increasing age (Table 2.1).

The smallest mature male measured 174 mm FL (age 4), and the smallest mature female measured 208 mm FL (age 6). Every sampled female over 306 mm was mature (n = 6) and every sampled male over 273 mm was mature (n = 13). Both males and females exhibited a tendency toward consecutive increases in proportion mature with increasing length (Table 2.1). There are a few decreases in proportion mature with increase in length for both males and females, but the trend still indicates increases in maturity proportions. These decreases are most likely a function of the precision with which the maturity proportions were estimated and the arbitrary length classes, but they could indicate a prevalent skip of a spawning year after first spawning.

Table 2.1. Sample size, interval mean, and maturity proportions of age and length data for cutthroat trout at Florence Lake , October 1997.

Interval	Female			Male		
Length (mm FL)	Sample Size	Interval Mean	Proportion Mature	Sample Size	Interval Mean	Proportion Mature
≤ 180	14	163.57	0.000	17	164.06	0.118
181-200	11	190.91	0.000	15	191.53	0.133
201-220	19	210.74	0.211	13	212.46	0.462
221-240	28	231.68	0.536	15	232.53	0.400
241-260	28	251.50	0.714	10	252.60	0.900
261-280	19	268.58	0.789	16	270.88	0.688
281-300	9	289.00	0.778	11	315.70	1.000
≥ 300	12	327.50	0.833			
Total	140			97		
Age						
4	8	4	0.000	14	4	0.143
5	14	5	0.000	18	5	0.167
6	24	6	0.375	19	6	0.474
7	30	7	0.433	17	7	0.471
8	35	8	0.714	11	8	0.909
9+	29	9.8	0.828	18	9.4	0.833
Total	140			97		

[1] To increase sub-sample size for the larger male cutthroat trout, the last two length intervals were pooled (>280 mm).

The logistic model was fitted to both the male and female maturity proportions in 20 mm length intervals (Table 2.1). While the visible fit would change with various arbitrary length intervals, the parameter estimates remained relatively consistent. The asymptotic maturity parameter m_∞ was not constrained to 1.00 (which translates to 100% of the fish being mature at a large size). Instead the parameter was estimated for supplementary control over the model. The logistic curve sufficiently modeled the maturity of both male and female cutthroat trout as a function of length (Figure 2.10). Males appear to mature at smaller size than females, and maturity gradually increases to the asymptotic maturity estimate of 100% (Figure 2.11). Females mature at a larger size than males and more abruptly enter into maturity at around 260 millimeters, up to the asymptotic maturity estimate of 80.2% (Figure 2.11).

The parameter estimates for the logistic maturity at length model along with associated standard error estimates (both bootstrap and the Hessian methods were calculated for comparison) and model statistics are given in Table 2.2. There appears to be considerable difference between the Hessian and the Bootstrap standard error estimates for the female maturity parameters as a function of length, with the Hessian estimates much smaller than the bootstrap. This dataset has a very low RSS for the given sample sizes (and hence a low $\hat{\sigma}$). In other words, the estimated maturity proportions in Figure 2.10 (top) are much closer to the predicted line than would expected by chance. The Hessian calculations assume this variability is typical and consequentially underestimate the standard errors of the parameter estimates. The bootstrap standard error estimates are

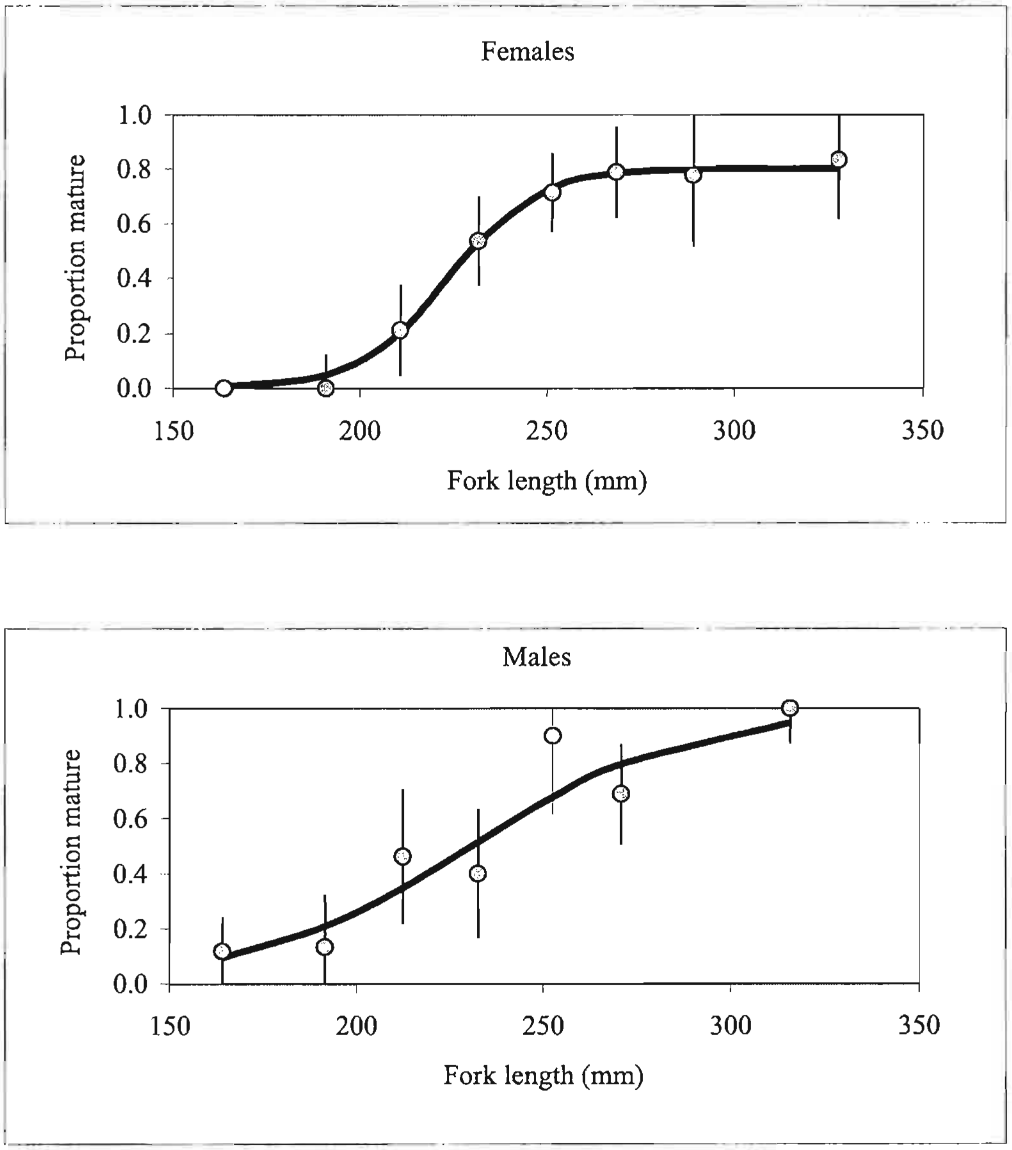
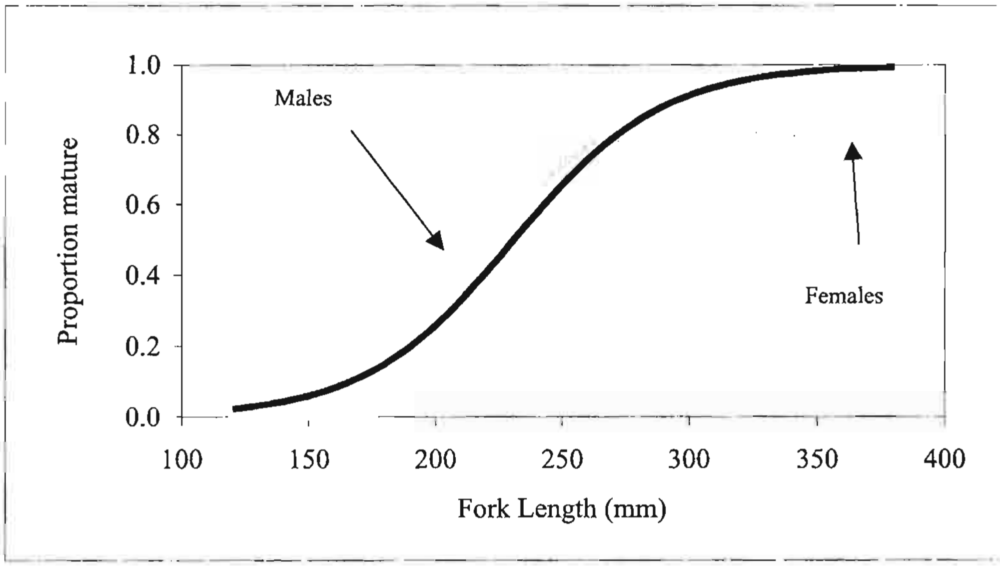


Figure 2.10. Logistic length at maturity models with estimated proportions mature and 90% confidence intervals for cutthroat trout at Florence Lake.



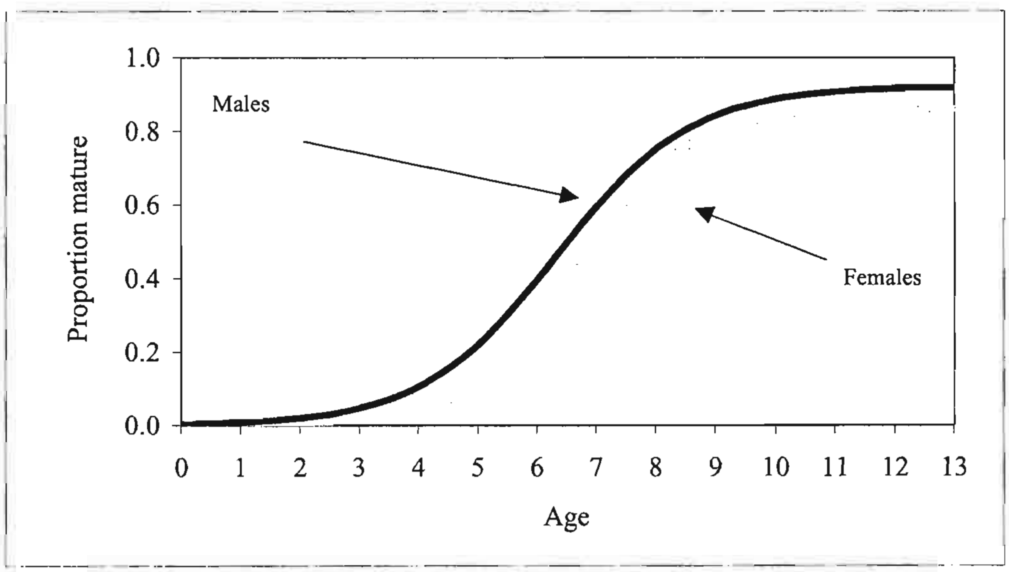


Figure 2.11. Logistic length and age at maturity models for male and female cutthroat trout at Florence Lake.

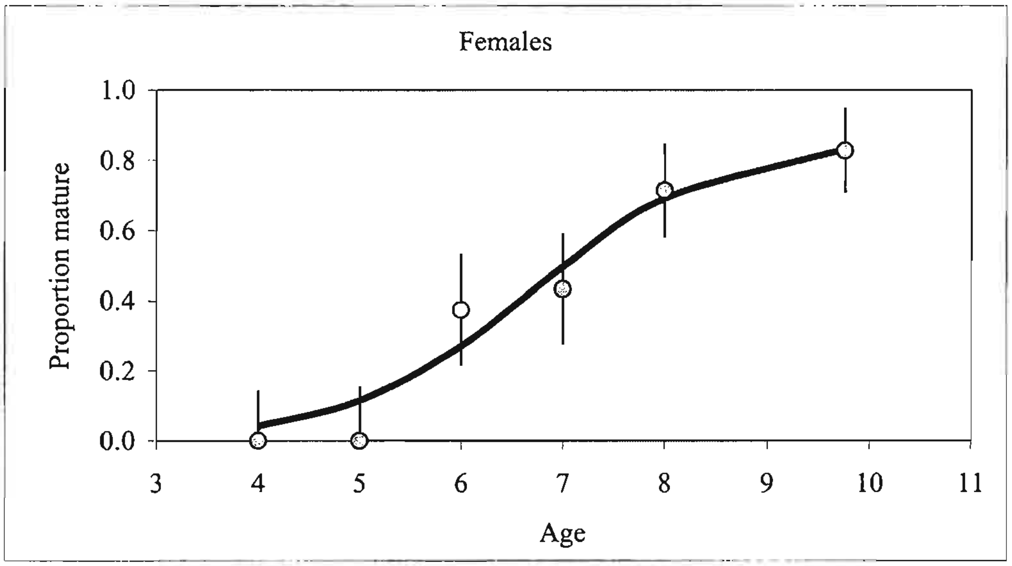
Table 2.2. Parameter estimates and variance statistics for logistic maturity model fitted to age and length at maturity data for coastal cutthroat trout at Florence Lake.

		Estimated Standard Error			
	Estimate	Hessian	Bootstrap		
Female Length					
m_∞	0.802	0.018	0.073	RSS	0.052
κ	0.084	0.008	0.048	$\hat{s}$	0.102
γ	223.719	1.261	6.095	n (intervals)	8
Male Length					
m_∞	1.000	0.248	0.070	RSS	1.172
κ	0.034	0.017	0.075	$\hat{s}$	0.541
γ	230.916	21.122	11.337	n (intervals)	7
Female Age					
m_∞	0.862	0.111	0.073	RSS	0.601
κ	1.088	0.359	0.397	$\hat{s}$	0.448
γ	6.719	0.396	0.295	n (intervals)	6
Male Age					
m_∞	0.921	0.182	0.081	RSS	0.741
κ	0.881	0.405	0.715	$\hat{s}$	0.497
γ	6.325	0.683	0.398	n (intervals)	6

robust to this and are therefore superior. Using Zar's (1974) method to test model variances, the null hypothesis of equal variances between sexes was rejected (P = 0.006). A significant difference in maturity parameters was detected between male and female cutthroat using a likelihood ratio test, under the different variance approach (Quinn and Deriso 1999: 169–171); (χ^2=16.8, P = 0.0007).

The logistic model was fitted to the maturity proportions at age for both males and females. Again, the asymptotic maturity parameter m_∞ was not constrained to 1. The logistic curve sufficiently modeled the maturity of both male and female cutthroat trout as a function of age (Figure 2.12). Males appear to mature at younger age than females (Table 2.1) and gradually maturity increased to the asymptotic maturity estimate of 92.1% (Figure 2.11). Females appear to mature at a slightly older age than males (Table 2.1) but maturity abruptly increases at age six, up to the asymptotic maturity estimate of 86.2% (Figure 2.11).

The parameter estimates for the logistic maturity at age model along with associated standard error estimates are given in Table 2.2. Differences between the Hessian and bootstrap estimates of parameter variance are not as large as that of the logistic maturity at length model parameters. Using Zar's (1974) method to test model variances, the null hypothesis of equal variances between sexes was not rejected (P = 0.650). A significant difference in maturity parameters was not detected between male and female cutthroat trout using a model comparison F-test (Quinn and Deriso 1999: 167–168); (F = 0.659, P



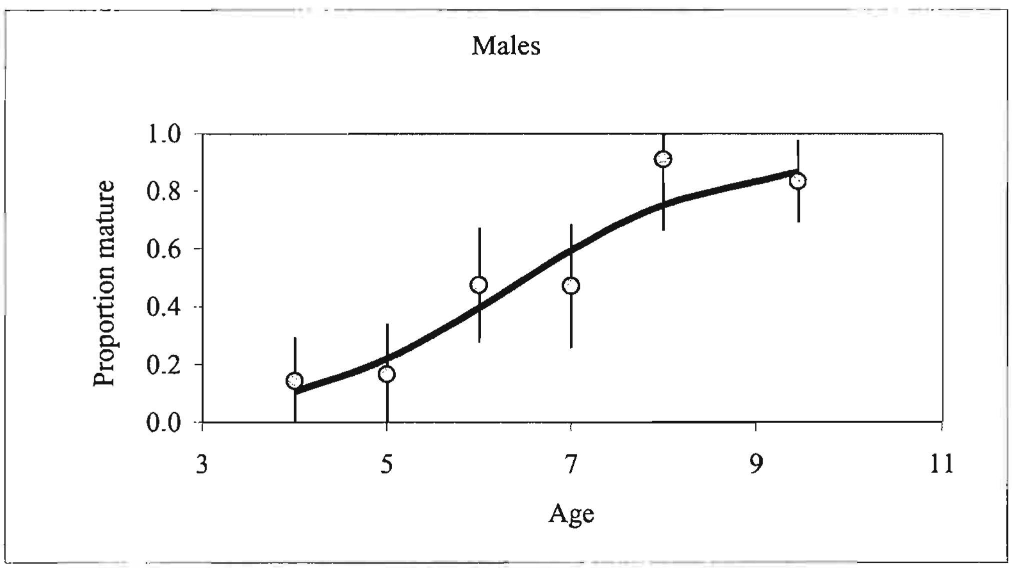


Figure 2.12. Logistic age at maturity models with estimated proportions mature and 90% confidence intervals for cutthroat trout at Florence Lake.

= 0.606). An F-test was used in this case, instead of the likelihood ratio test used for the length at maturity analysis, because the F-test's assumption of model variances equal across the male and female data sets was not violated.

Maturity of cutthroat trout at Florence Lake was also estimated as a function of total length (inches), in addition to fork length, because the size-based regulations governing harvest of trout in Southeast Alaska are based on this unit of measure. A linear regression of total length on fork length (mm) was performed. The regression ($L_{TL} = 8.16 + 1.01L_{FL}$) was highly significant ($R^2 = 0.99$, $P < 0.00005$). There was no significant difference between males and females. Utilizing these regression statistics and metric to standard unit conversions, the male and female cutthroat maturity logistic model was simply converted to total length in inches (Figure 2.13). Male cutthroat start maturing at around 7 and females around 9 inches. In combination, approximately 50% of the population is mature at 9.5 inches. Reference lines on Figure 2.13 show 11 and 12 inch size ranges which correspond to the 2000 and 1994 minimum size limits, respectively. Lowering the minimum size limit from 12 to 11 inches in 2000 corresponds to almost no change in the male proportion and only a small change in the female proportion mature of the cutthroat trout at Florence Lake. The total length at maturity and its relation to the regulations will be discussed further in chapter three.

Fecundity

Fecundity of cutthroat trout at Florence Lake increased with both increasing age and

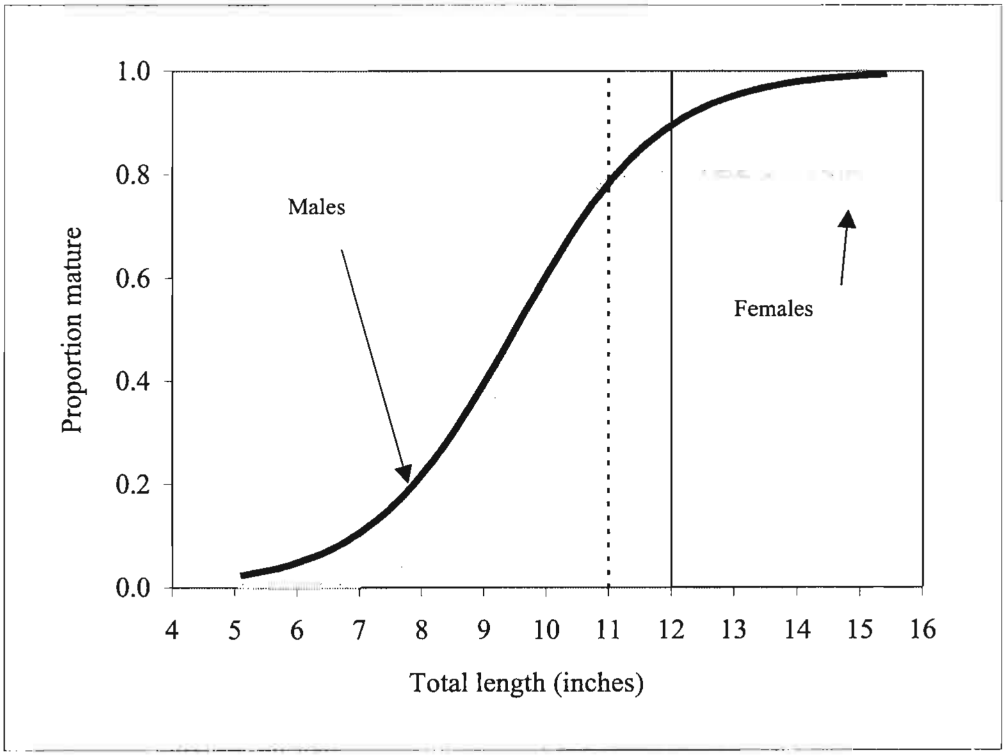
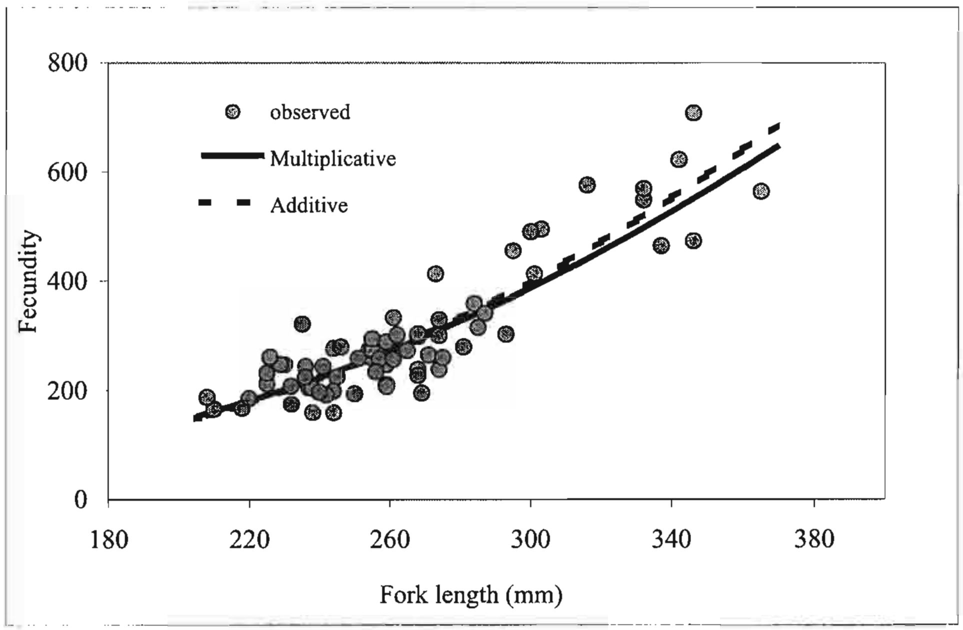


Figure 2.13. Logistic length at maturity models for male and female coastal cutthroat trout at Florence Lake. Reference lines show both the 12 and 11-inch total length ranges

length, but was better predicted and much less variable as a function of length. Linear regressions of fecundity on age and fork length gave R^2 values of 0.60 and 0.79 and significant slopes ($P < 0.005$). Fish body weight and ovary weight were also good predictors of fecundity with linear regression R^2 values of 0.83 and 0.78 respectively and both slopes significant ($P< 0.005$).

Fecundity was modelled as an allometric function of length, and a multiplicative error structure was chosen after comparison with the additive. Both error structures yielded nicely fitted curves to the data (Figure 2.14). Examination of the residuals plotted against the predicted fecundity suggested a very slight increase in spread as fecundity increased, for the additive error structure. Examination of the multiplicative error structure residuals (natural log transformed), indicated that the variation slightly decreases with increasing fecundity (Figure 2.14). The standard errors for the additive error structure's allometric parameter estimates were both slightly lower than the variation estimated by the multiplicative error structure (Table 2.3). However, the lower confidence limit of α (additive error) contained zero, resulting in the invalidation of that model.

The 95% confidence intervals for the curvature parameter β do not contain value 3, suggesting that the isometric model (allometric model with $\beta = 3$) is not appropriate. A length-weight relationship was established with the allometric growth model (Figure 2.15), and both multiplicative and additive error structures yielded $\hat{\beta}$ values slightly larger than 3 and statistically different (Table 2.3). The discrepancy between the length-



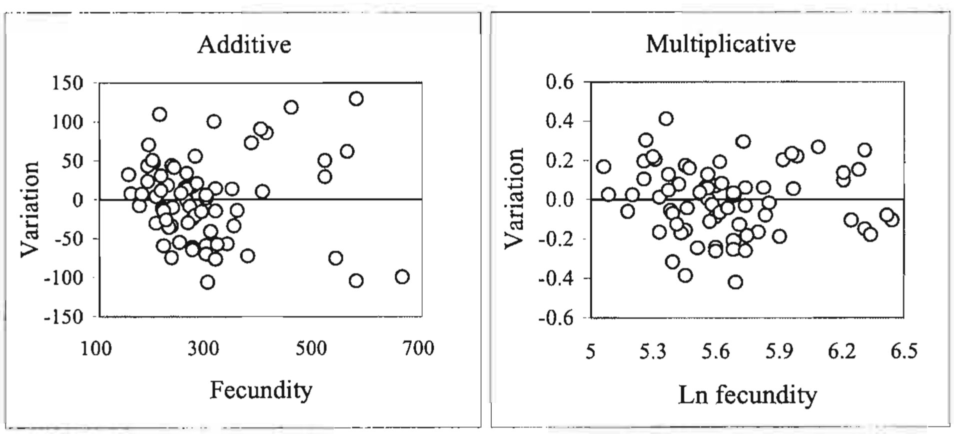


Figure 2.14. Allometric length-fecundity model showing both additive and multiplicative error structures and residual plots for cutthroat trout at Florence Lake.

Table 2.3. Allometric fecundity, length, weight, and gonad volume relationship model parameter estimates and standard errors for cutthroat trout at Florence Lake.

	Allometric relationship					
	Length and fecundity		Length and weight		Length and gonad volume	
Statistic	Add.[b]	Mult.[c]	Add.[b]	Mult.[c]	Add.[b]	Mult.[c]
$\widehat{\alpha}$	0.0001554	0.0003305	0.0000062	0.0000056	0.0000030	0.0000004
SE $\widehat{\alpha}$	0.0001230	0.0003106	0.0000010	0.0000007	0.0000042	0.0000007
LCL [a]	-0.0000901	0.0000507	0.0000042	0.0000044	-0.0000055	0.0000000
UCL [a]	0.0004009	0.0021563	0.0000083	0.0000072	0.0000114	0.0000099
$\widehat{\beta}$	2.588	2.450	3.059	3.075	3.858	4.189
SE $\widehat{\beta}$	0.137	0.169	0.029	0.023	0.248	0.281
LCL [a]	2.314	2.114	3.001	3.030	3.360	3.624
UCL [a]	2.862	2.787	3.116	3.121	4.356	4.754
n	70	70	237	237	52	52
df	68	68	235	235	50	50
t	1.995	1.995	1.970	1.970	2.009	2.009

[a] LCL and LCL are the lower and upper bounds of the 95% confident interval.

[b] Additive error model.

[c] Multiplicative error model.

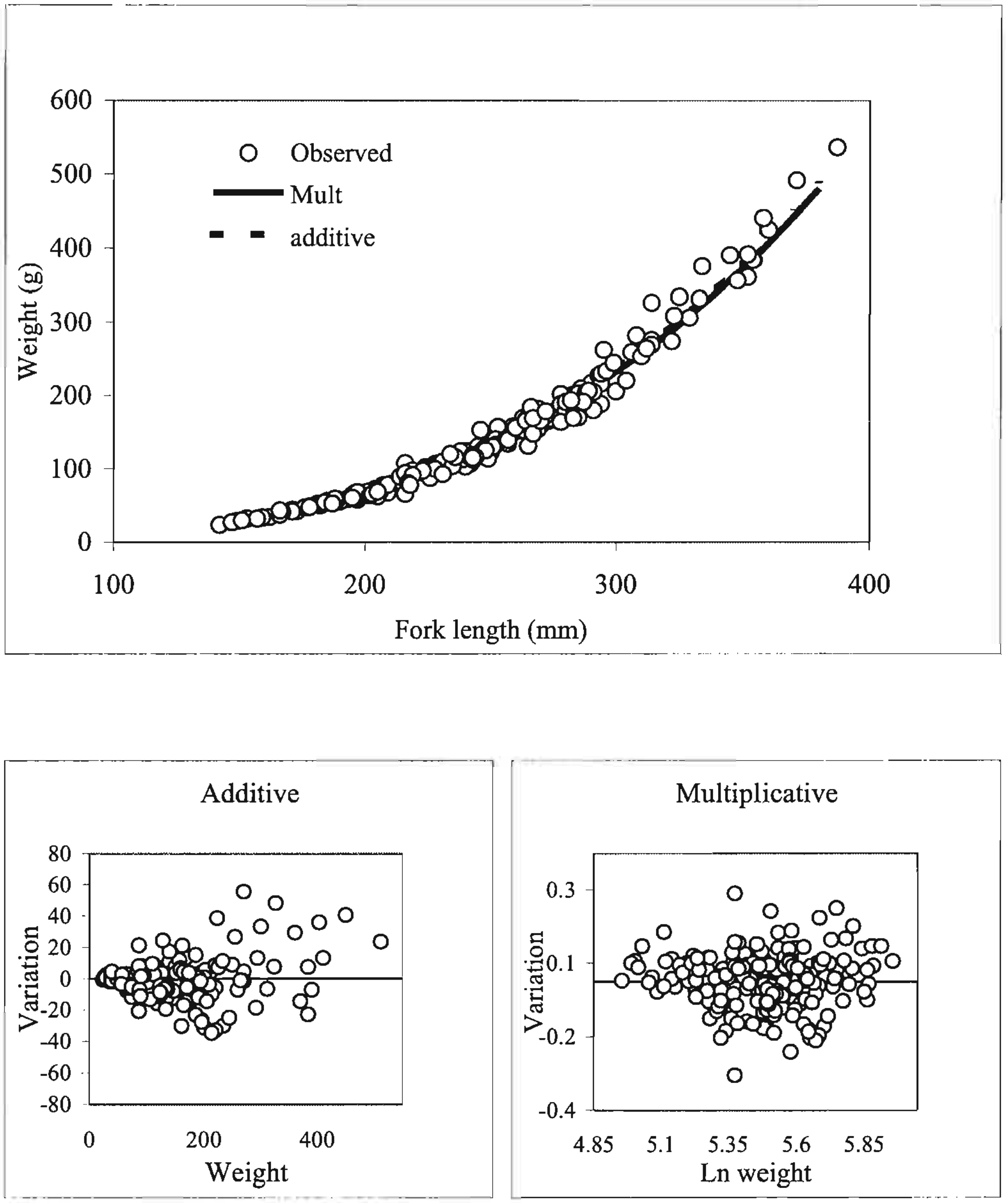


Figure 2.15. Allometric length-weight model showing both additive and multiplicative error structures and residual plots for cutthroat trout at Florence Lake.

fecundity and length-weight curvatures suggests that the fecundity was less than would be expected, especially for the larger fish. Fecundity increases with increasing size of cutthroat; however, due to the production of larger eggs, relative fecundity decreases in the larger fish (Behnke 1992).

An allometric relationship between length and a gonad volume was constructed to further analyze this biological process in trout (Figure 2.16). Gonad volume (Vg; in mm^3) was estimated by multiplying fecundity by an estimate of the average ovum volume (assuming spherical ova),

$$Vg = \tilde{f}\frac{4}{3}\pi\left(\frac{\text{avg. ovum diameter}}{2}\right)^3. \tag{2.12}$$

The regression yielded a curvature parameter β = 4.189 (Table 2.3) which is a much steeper curve than for either the length-fecundity and length-weight allometric relationships. This result (in addition to Figure 2.4) suggests that as the cutthroat trout grows larger, a quite significant trade-off of fecundity for egg size is made.

Growth

The various cases of the Schnute growth model were fitted to the cutthroat age and length data. A nonlinear least squares optimizing routine in Excel was used to minimize the residual sum of squares (RSS). The user defined model values of τ_1 and τ_2 were fixed at

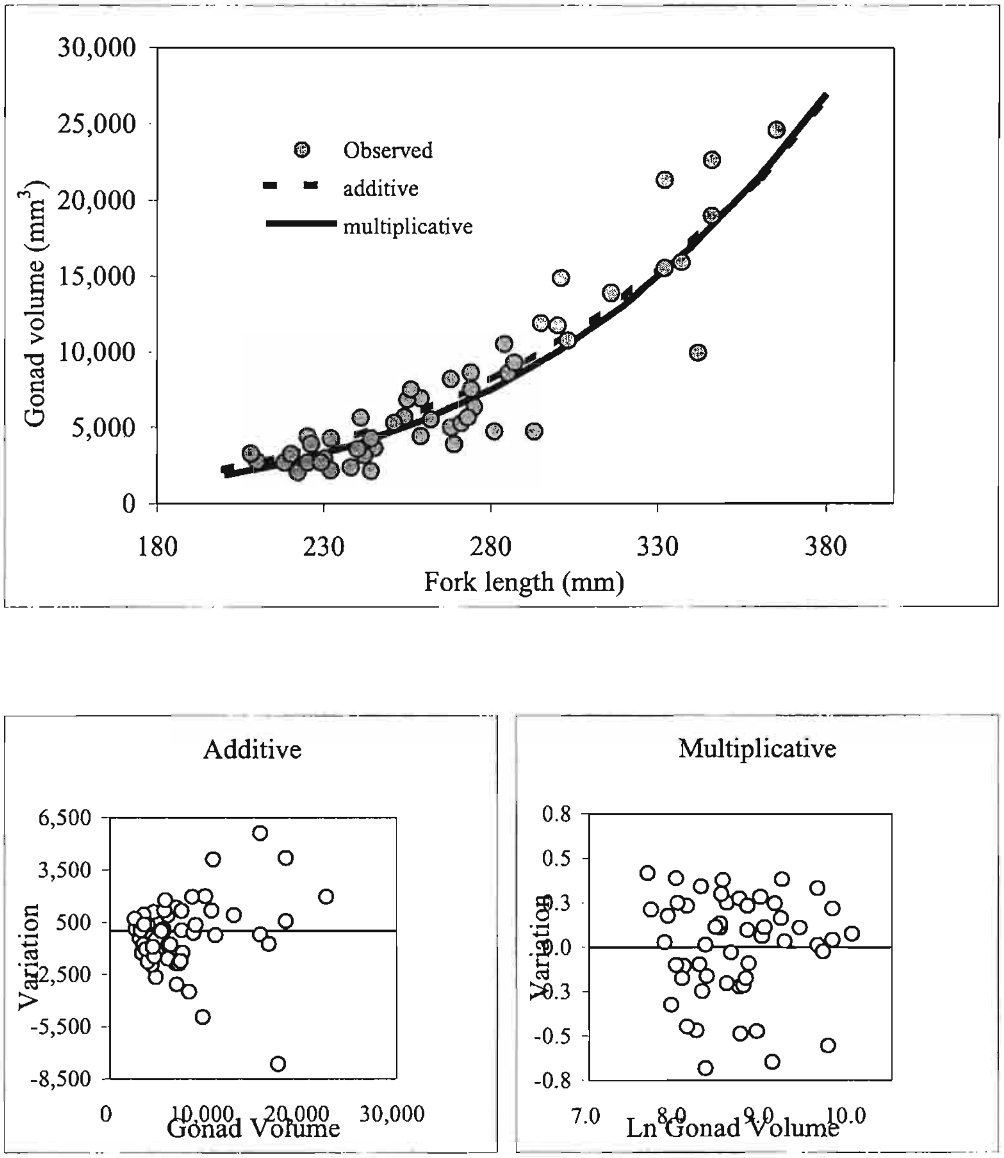
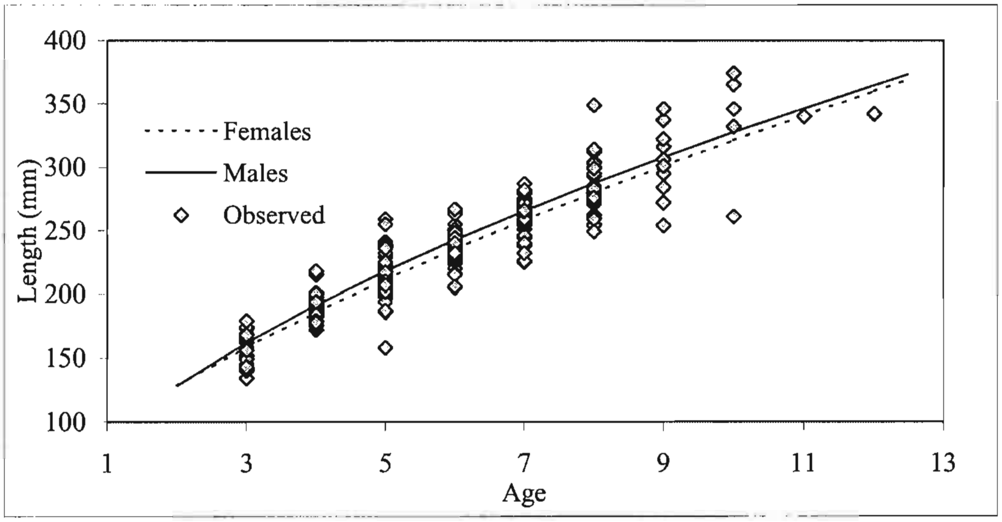


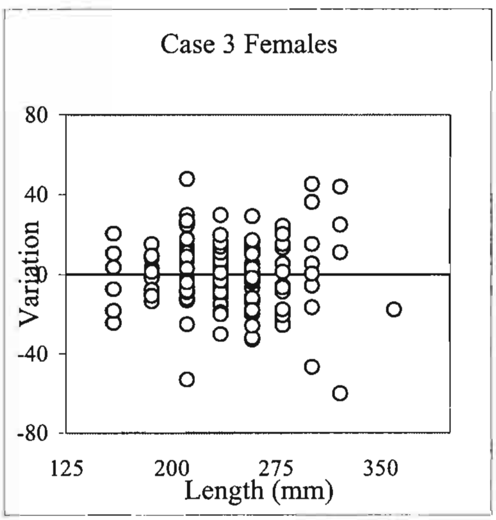
Figure 2.16. Allometric length-gonad volume model showing both additive and multiplicative error structures for cutthroat trout at Florence Lake.

3 and 11, respectively, which were the youngest and oldest ages sampled common to both female and male data sets. Male and female cutthroat were analyzed separately assuming both an additive and a multiplicative error structure. Visual inspection of model fit and the model residuals plotted against predicted length showed that the variance was not constant (heteroscedasticity) with the additive error structure (Figure 2.17 and App. Figures A.1–A.3); variance appeared to increase (very slightly) with increasing length. Inspection of the multiplicative error structure model fit and residuals revealed a more solid band of variation about the fitted line (Figure 2.18 and App. Figures A.4–A.6) and established the multiplicative as the more apt error structure, although both fitted the data comparably.

In all analyses (additive and multiplicative), Schnute growth model cases 2, 3, and 5 were not significantly different from the full model (case 1) (App. Tables A.3–A.5). The null hypothesis that case 4 was the same as the other models was consistently rejected in all circumstances. Analysis of residual plots, Schnute model comparison F-tests, and the RSS showed case 3 to be superior to cases 2 and 5 for males, females, and a pooled sex model (App. Tables A.3–A.5). Since case 3 was not significantly different than case 1, and has fewer parameters, case 3 (multiplicative error) was chosen as the best model for cutthroat trout growth at Florence Lake.

Overall growth of male and female cutthroat trout using case 3 (multiplicative error) (Figure 2.19) was found to be statistically different, however no difference was detected





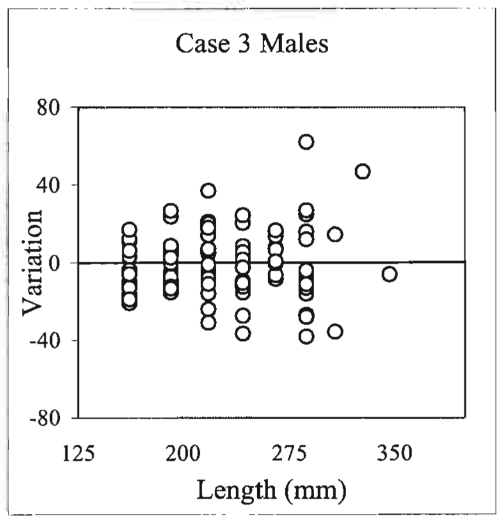
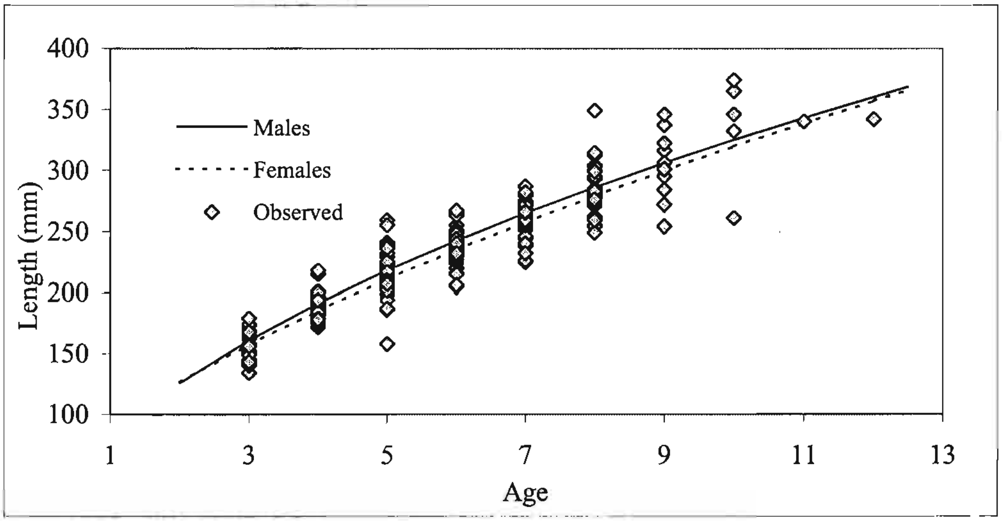


Figure 2.17. Schnute growth model (case 3 additive error) fits to male and female cutthroat trout age and length data, and associated residual plots, Florence Lake.



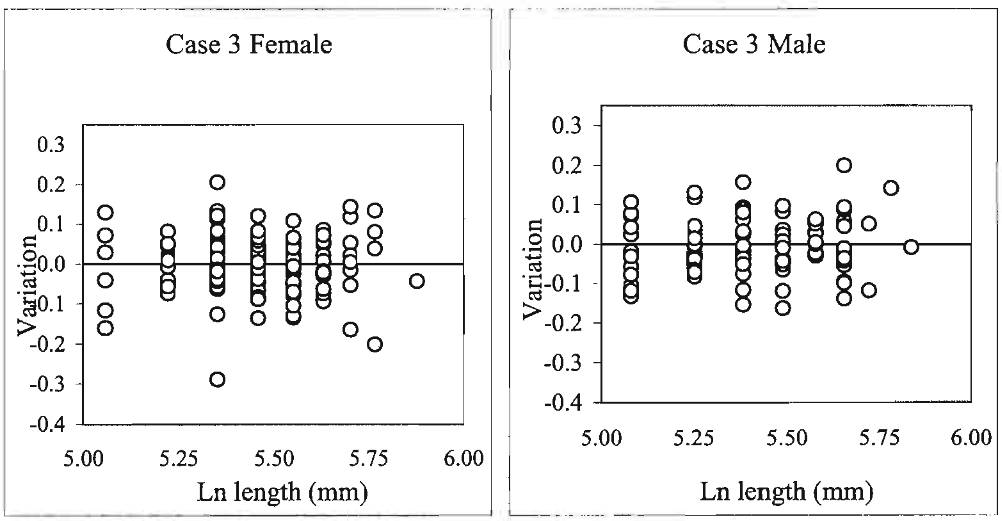


Figure 2.18. Schnute growth model (case 3 multiplicative error) fits to male and female cutthroat trout age and length data, and associated residual plots, Florence Lake.

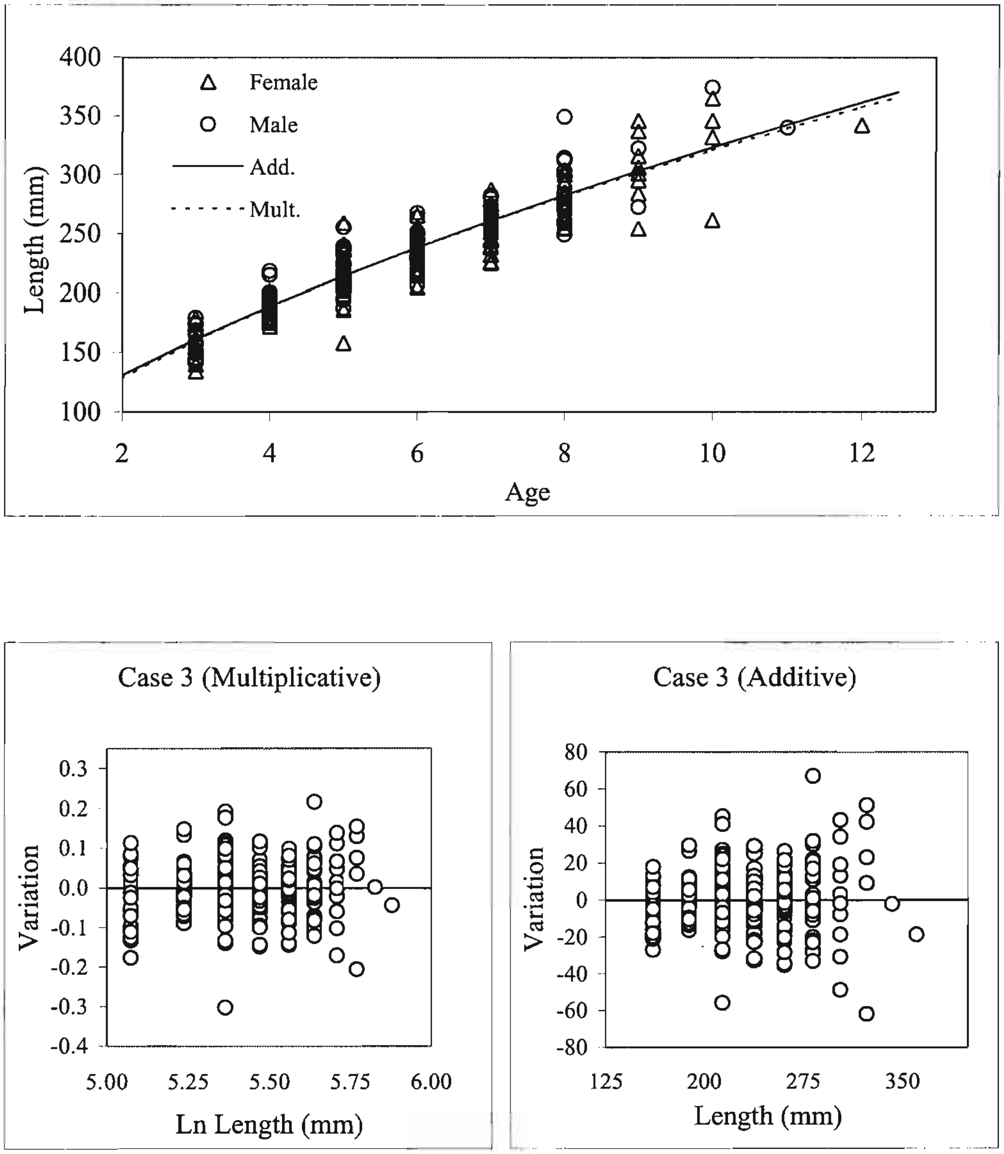


Figure 2.19 Schnute growth model (case 3 multiplicative error) fits to cutthroat trout (sexes pooled) age and length data, and associated residual plots, Florence Lake.

between the distinct parameters of the two. Using Zar's (1974) method to test model variances, the null hypothesis of equal variances was not rejected (P = 0.99). By assuming equal variances, an F-test analogous to Schnute's model comparison and to likelihood ratio tests (Quinn and Deriso 1999) rejected the null hypothesis that male and female parameters for Case 3 were equal (P = 0.043) (App. Table A.6). Differences in the specific parameters l_1, l_2, and γ between the sexes were tested with the Fisher-Behrens z statistic. The null hypothesis of equality was not rejected for each parameter with $P >$ 0.45 (App. Table A.6). The total parameter test that parallels that of the single parameter test using the Fisher-Behrens z-statistic is the Hotelling T^2 test. This test rejected the null hypothesis of equal parameters between the male and females for case 3 ($P < 0.05$) for both equivalent and different variance approaches (App. Table A.7).

This appears to be a situation where a significant statistical difference is detected between the growth of male and female cutthroat trout, yet little visible difference in model appearance (Figure 2.19) suggests that there is not a functional or a biological distinction (i.e., the power of the test is high). Since no meaningful difference was found between the single parameters, the resulting pooled sex model will be utilized in the analysis of sustained yield (Chapter 3). For commonality with other studies, the widely used LVB growth model (case 5) will be utilized in chapter three; case 5 fit the data similar to case 3 and was also not significantly different than case 1.

DISCUSSION

Maturity (spawning the next spring) is an essential parameter for effectively estimating the reproductive potential of the population. Sampling in the fall was successful for estimating maturity. Winter sampling would be extremely difficult due to inclement weather and a frozen lake cover. As soon as the winter ice cover breaks up, warming of the water signals the cutthroat spawning instinct (Behnke 1992). Even if the cutthroat trout have not yet entered the spawning tributaries, they are most likely already forming spawning aggregations that would prevent a random sample from being drawn from the lake (Rosenkranz et al. 1999). Jones (1981) found sexually mature cutthroat to be most profuse near the main inlet creek in April at Florence Lake.

During the summer, those fish that are to spawn next year will develop their gonads, mostly in late summer and into the fall. By autumn, those cutthroat trout gonads should be in an advanced stage of development because energy stores during winter are spent on body maintenance and not for gonadal development (Behnke 1992). This development was observed throughout the summer at Florence Lake and not until September was there conspicuous difference between mature and immature gonads. The difference in October was even much more pronounced. Examining gonads at this time or later in the fall eases the maturity determination significantly.

While sampling in the fall eases the maturity determination, cutthroat trout gonads must still be carefully examined. This often takes place in unfavorable field conditions unlike that of a laboratory. Lighting was found to be very important in examination. Color of ovaries played no part in determining maturity; however, color was very important in distinguishing between immature males and females. The gonads of these trout were minute and close inspection in good lighting was necessary to discern the orange of the female or thread-like whiteness of the male. Maturity samples may be preserved to allow post-examination. However, preservatives (e.g., 10% buffered formalin) should not be counted upon to retain the original color upon removal from the fish. Preserving the female ovaries is beneficial for post examination because they can be viewed with other samples for comparison of maturity stages and possibly to validate field determinations. Errors made in the field notes can be corrected with re-examination.

The GSI developed for Florence Lake cutthroat trout was extremely accurate in the separation of the females that had a relatively large percent of their body weight invested in the ovaries and those that did not. The clear distinction of the two groups when plotted against length would actually allow for a quantitative method of maturity determination upon returning to the lab and measuring ovary weights. At Florence Lake, those fish with GSI's above 0.018 in October would be considered mature. However, due to the time invested in extracting the ovaries from a cutthroat trout and the ease at which determination could be made, dissection is the best time to do this (assuming adequate lighting is available). The GSI can be useful in identifying ovaries that are on the borderline of mature and immature. In examining the GSI, there were two distinct groupings of female cutthroat: those that have developed gonads and those that have not.

Southeast Alaska is in the northern range of the coastal cutthroat trout, water temperature is cold, and growth is slow. It is doubtful that these fish would sacrifice energy stores for gonadal development if they were not going to spawn the next spring.

Female cutthroat trout begin maturing at a larger size than males, but maturation is more abrupt than the gradual transition for males. Downs et al. (1997), studying Westslope cutthroat trout in Montana, found this same difference between male and females in the maturity transition. Female cutthroat trout at Florence Lake first started maturing at about 208 mm and males at around 174 mm. Leeuw (1987), studying the coastal cutthroat trout at the Mosquito Lake system in the Queen Charlotte Islands, found the smallest mature cutthroat trout to be 220 mm; however this system supported a much larger average size of fish. Few studies have been published on quantitative maturity at length for resident cutthroat trout.

Considering the more abrupt transition to maturity when modeled as a function of length, length is probably a better predictor of maturity than age. Asymptotic maturity using length for males and females was estimated as 1.000 and 0.802, and asymptotic maturity using age was estimated as 0.921 and 0.862, respectively (Table 2.2). These data suggest that males reach a greater proportion mature at a large size and old age and that there is a presence of skip spawning in large and old cutthroat trout of both sexes, particularly females. Much of the difference between the asymptotic maturity parameters (both male and female) of the age and length models is due to the "plus" grouping (age 9+) in the maturity at age model. The "plus" group in the female data represented 29 fish and in the males represented 18 fish (Table 2.1). Also influencing these differences is the error associated with estimating a population proportion and the variability in length at age.

The residual eggs also yield interesting proof that some fish, upon reaching maturity, will spawn in back to back years and conversely, some fish, in spite of spawning before, will skip a spawning year. While cutthroat are iteroparous, skipping a spawning season once reaching maturity has been cited in the literature (Giger 1972; Tomasson 1978; Trotter 1989). It is likely that skip spawning increases with increasing latitude and decreasing growing seasons. Volodin (1980) studied resorption of unspawned eggs for 30 different species of fish and determined it might be advantageous to the fish by recovery of the nutrients.

Published studies on unshed eggs in trout and salmon spawning suggest that unshed eggs are a function of density. A study of fecundity of brook trout at 71 lakes in Nevada found large unattached eggs (residual eggs) to be more prevalent in females from lakes showing the worst crowding and stunting (Hall 1991). In addition, egg retention in sockeye was positively correlated to the density of females in the spawning stream (Mason and West 1987; $P < 0.001$). Florence Lake is recognized in Southeast Alaska as having one of the larger populations of resident cutthroat trout. With a barrier falls limiting the outlet creek availability to the cutthroat, conditions are good for high spawning densities in the three major inlet creeks.

Much effort was expended to sample larger cutthroat in Florence Lake and very few fish in the lake are outside the sample ranges. In the cutthroat trout mark-recapture experiments from 1991 to 1994, only 23 of the 12,000+ sampled cutthroat were larger than the maximum size sampled in the maturity study. Thus, the less than 100% maturity reached for the larger fish is most likely true and not a product of the sample size at length.

From the maturity at age model, the age at which 50% of the female cutthroat are mature is 7.01 and age at which 50% of the male cutthroat are mature is 6.52 (6.83 for both sexes in combination). From the raw data, not until age 8 did either males or females have a majority proportion mature (Table 2.2). When cutthroat males or females mature at different ages, males tend to mature sooner than females (Behnke 1992). Fish over age 9 were pooled. Even in these older age classes (average of age 9.8 for female and age 9.4 for male), only 82.8% and 83.3% of the cutthroat were mature, also indicative of occasional skip spawning at old ages.

Yellowstone cutthroat trout in Yellowstone Lake were found to spawn first at age 3, although age 4 was more common (Bulkley 1961). Westslope cutthroat trout males first matured at age 2–3, while females first matured at age 3-4 (Downs et al. 1997). Anadromous cutthroat trout in Washington first spawned at age 4-5 and very few females mature before age 4 (Fuss 1982). Lake dwelling cutthroat trout in Washington first spawn at age 3, but more commonly age 4 (Pierce 1984). Cutthroat trout in Southeast Alaska typically mature at 5-6 years old (Jones 1982).

While there is a paucity of information on age at maturity, it is clear that the age at maturity for Florence Lake cutthroat trout is one of the older documented. This is not surprising, considering the northern location and relatively slow growth and old ages attained by cutthroat at Florence Lake. An older age at maturity is a characteristic of a cutthroat population with a long lifespan (Behnke 1992). Ages of 14 and 15 years have been recorded for resident cutthroat trout in Southeast Alaska (Jones 1978) and fish of this age may occur at Florence Lake (a 299 mm cutthroat was tagged in August 1990 and re-captured during the maturity study in October 1997, measuring 453 mm).

Fecundity as a function of length (Figure 2.14, Table 2.3) is similar to that in published literature on coastal cutthroat fecundity. Fecundity for cutthroat trout in Southeast Alaska ranges from 486 for a 340 mm fish to 2,286 for a 460 mm fish (Jones 1976). The average fecundity of four cutthroat trout in British Columbian between 356 mm and 375 mm was 705 eggs (Leeuw 1987). In Washington State, the fecundity of female coastal cutthroat from 200 mm to 430 mm in length ranged from 226 to 4,420 eggs (Johnston and Mercer 1976). Fecundity reported for Westslope cutthroat trout in Montana was considerably greater at length; average fecundity of 11 Westslope cutthroat trout averaging 218 mm in length was 459 eggs (Downs et al. 1997).

For Florence Lake, not only did the fecundity increase with length, but the average ovum diameter did as well. This is important because the survival of brown trout is significantly greater for fry from large eggs than it is from small eggs under natural conditions (Bagenal 1969). Also, chum salmon eggs that are larger produce larger embryos and a larger size at emergence (Hayashizaki et al. 1995). Thus the larger cutthroat trout at Florence deposited not only more eggs but perhaps spawn fry with a greater chance of survival. This aspect should be explicitly incorporated in population modeling. The importance of the large female cutthroat trout spawners is also emphasized by the precipitous increase in gonad volume with increasing length, more so than fecundity. For example, a 350 mm cutthroat will have about 2.4 times the fecundity, but 4 times the gonad volume of a 250 mm fish.

Florence Lake cutthroat trout scales were known to be difficult to age (Ericksen 1997; 1999), and this fact was reflected in the somewhat low agreement between my two readings (64.6%). However, between 2 and 4 scales were viewed per sample, which would sacrifice some precision for accuracy. The noisy scale pattern present in Florence Lake cutthroat trout has been documented in the past; the scales of cutthroat at Florence Lake do not have obvious annuli like those from Turner Lake (Jones et al. 1990). Otoliths may prove to be more accurate, but preliminary attempts at using otoliths in this study indicated the otoliths were as difficult as the scales to read. That being the case, having to kill the fish to acquire the structure is not a prudent trade-off.

A departure (increase) from the smooth curve after age 7 or 8 on the scatterplot of circuli versus age (Figure 2.8) probably indicates that the fish over that age are older than estimated; this is one reason why the maturity in the larger fish was modeled with a plus group. On the other hand, a biological reason for this increase in number of circuli could be a change in feeding habits and growth upon reaching a certain size (Behnke 1992) and ability to feed on a new prey item (e.g. piscivory) such as the kokanee, sculpin, or stickleback present in Florence Lake.

The growth of cutthroat trout at Florence Lake is relatively slow and the trout's lifespan long. The best growth model was Schnute's case 3 (multiplicative). Unlike cases 1 and 2, case 3 does not have an inflection point or an asymptote which seems unnatural in describing the growth of trout. However, the absence of both young and very old fish apparently negated the need for an inflection point or asymptote in describing the growth of cutthroat trout within a certain range. The absence of young fish sampled during the maturity study was due to the reduced samples needed for the low maturity proportions encountered in small fish. The absence of older fish (over 12 years old) in the sample was due to the very few fish which actually attain this age and possibly the underestimation of age which may occur in very large fish.

Compared to other resident cutthroat trout populations in Southeast Alaska and correcting for the time of year sampled, average length at age appears considerably less at Florence Lake than Petersburg Lake (Jones 1976), Hasselborg Lake, Thoms Lake, and Virginia

Lake (Jones 1980). Cutthroat trout at Florence Lake were found to be significantly smaller at age than cutthroat trout at both Turner and Auke Lakes in Southeast Alaska (Ericksen 1997). Ericksen also modeled growth of Florence Lake cutthroat trout with the various cases of the Schnute's growth model and found the best additive model to be case 3 and best multiplicative model to be case 2.

Some differences exist between the growth analysis reported here and in Ericksen (1997). Ericksen utilized very young and small cutthroat trout that were not targeted for my length and age at maturity study, and in addition had a larger number of cutthroat trout over 350 mm to better model the upper portion of the growth curve. All samples collected in the main portion of this study were collected in late October, while Ericksen's samples were collected in April through June (much of the yearly growth occurs between June and late October). In addition an aging error model was utilized by Ericksen to improve accuracy of the age estimates.

The ages estimated in this study, correcting for time of year collected, appear to be positively biased by one year up to about age 6 or 7 compared to Ericksen. At that point much of the difference in age/length disappear. The growth analysis in this study estimated 12 age classes up to approximately 350 mm as did Ericksen (1997). Nevertheless, the application of the maturity at length model from this study to Ericksen's more rigorous growth analysis, (sexes combined), results in the age at which 50% of the cutthroat population is mature being approximately 7 years old, roughly equivalent to this study's estimate of 6.8. The growth analysis in this report did not attempt to duplicate the rigorous analysis by Ericksen (1997), but to utilize the criteria set forth by Ericksen (1999) in aging cutthroat trout in Southeast Alaska.

I recommend that future research be directed to aging cutthroat trout using otoliths. Also, study of egg viability as a function of egg size in cutthroat trout would add substantially to the ability to model and manage trout populations. The complication of studying this unique fish is that many cutthroat spend their entire life geographically and reproductively isolated from any other cutthroat trout stock and also obtain vastly different sizes and growth rates. Thus information on one system is not easily translated to others.

CHAPTER THREE: SUSTAINED YIELD

INTRODUCTION

Daily creel (bag) limits and maximum size limits have been used to regulate trout harvest in Southeast Alaska since the 1940's (Table 1.1). In 1994, a minimum size limit (MSL) of 12 inches (305 mm) was established to permit a "high percentage" of females to spawn before being susceptible to angler harvest (Gresswell and Harding 1997). At that time, minimal age- and length-at-maturity information existed on cutthroat trout in Southeast Alaska, especially for non sea-run populations.

The Florence Lake cutthroat trout maturity study described above in Chapter 2 was part of an ADF&G project to estimate age and length at maturity for 21 cutthroat trout lakes in Southeast Alaska, both anadromous and potamodromous, sampled during the fall of 1997 and 1998. The methods, rationale, and information acquired during my study at Florence Lake contributed to the logistical planning and data analysis of the other lakes' maturity data. As a result of that investigation, the Southeast trout regulations were amended in 2000 with the pertinent change being a reduction in the MSL from 12 to 11 inches (Table 1.1). The biological premise of this 11-inch (279 mm) MSL is to protect juvenile steelhead and cutthroat before ocean migration and protect 60% of all cutthroat trout until they have a chance to spawn at least once (ADF&G regulations 2003).

The importance of the region-wide MSL is that it provides a practical, cost effective way to manage the many cutthroat trout systems in Southeast Alaska without detailed biological data on a lake-by-lake basis. Because of the diversity of management situations, several exceptions to this new region-wide MSL regulation were provided (Table 1.2). However, it seems prudent to make the regulations as robust to the biological factors as possible.

The State of Alaska mandates that fish populations be managed on a sustainable yield basis. Studies on sustained yield determination of Southeast Alaska trout populations were limited in the past, but have recently become more common. Erickson (1997) conducted an analysis of sustained yield of coastal cutthroat trout in Southeast Alaska, but did so without knowledge of maturity and fecundity. Der Hovanisian (1994) evaluated sustained yield of introduced rainbow trout at Blue Lake reservoir in Sitka using a per recruit model and estimating the fishing mortality ($F_{x\%}$) which reduces the spawning stock abundance per recruit to x% of its unfished spawning abundance per recruit. A sustained yield analysis of Dolly Varden in Chilkoot Lake near Haines was also conducted (Ericksen 2000). Clark (1993) found that $F_{35\text{-}40\%}$, which is the fishing mortality that results in spawning stock biomass 35-40% that of the unfished biomass on a per recruit basis, is frequently near F_{msy} for a variety of life history parameters and variable recruitment. With little or no knowledge of the recruitment processes for cutthroat trout in Alaska, this study focused on a sustained yield determination limited to a biological reference point (BRP) conveyed as a rate of fishing mortality (F).

The goal of this analysis is to evaluate the sensitivity of the Florence Lake cutthroat trout population to harvest as a function of different MSL's. This was accomplished via a per recruit analysis with selectivity being a function of the MSL. The analysis was conducted with both an age-based method and a length-based method. The age-based method follows the general form of Quinn and Szarzi (1993) and Quinn and Deriso (1999; ch. 11) for determining sustained yield of a recreational fishery. The length-based per recruit analysis is an adaptation of a length-based population model (Quinn et al. 1998) for hard-to-age invertebrates, with the addition of maturity and fecundity information to provide spawning biomass and egg production outputs.

A length-based model may produce a more accurate representation of cohort dynamics than the traditional age-based method (Shepherd and Idoine 1993). With the difficulty in aging, the MSL obviously being based upon length, and maturity and fecundity probably being better predicted by length than age for cutthroat trout, the merits and results of a length-based analysis should be appraised and compared to the age-based method. Very few length-based per recruit analyses have been published. The approach developed in this study will have the benefit of being applicable to other species and types of sport fisheries.

OBJECTIVES

1) Compare maturity data from cutthroat trout at Florence Lake to the objective of the current Southeast Alaska general trout regulations. Null hypothesis: The goal of

protecting 60% of cutthroat trout until they have a chance to spawn at least once will not be met for Florence Lake.

2) Analyze sustained yield for Florence Lake cutthroat trout by examining the sensitivity of population to different MSL's. Null hypothesis: There will be no significant difference in the fishing mortality estimates of sustained yield for the age-or the length-based per recruit analyses.

METHODS

Southeast Alaska trout MSL

The goal of the trout MSL in Southeast Alaska is to allow a majority of female (and hence all) cutthroat an opportunity to spawn at least once before being susceptible to angler harvest. In chapter two, total length (inches) at maturity was estimated for both male and female cutthroat trout at Florence Lake (2.13). The proportions of both male and female Florence Lake cutthroat that are mature at 12-inch (305 mm), 11-inch (279 mm), 10-inch (254 mm), and 9-inch (229 mm) total length MSL's are qualitatively assessed relative to the goal of the Southeast Alaska trout regulations.

Per recruit analysis

Age-based model

The basic configuration presented by Quinn and Szarzi (1993) for determining sustained yield of a recreational fishery on an age-based per recruit basis was employed. The following life history parameters and relationships were used in the analysis:

Let

N_a = abundance at age a

M = natural mortality

s_a = angler selectivity at age a

$\tilde{f}_a$ = gross fecundity of a mature female at age a

Vg_a = gonad volume of a mature female at age a

m_a = proportion of females mature at age a

F = full recruitment fishing mortality

$F_a = s_a F$ = fishing mortality at age a (3.1)

$Z_a = M + F_a$ = total instantaneous mortality (3.2)

$S_a = \exp(-Z_a)$ = survival at age a. (3.3)

The general recursion equation for abundance is:

$$N_{a+1} = S_a N_a \ , \quad (3.4)$$

where abundance at age a+1 is a function of the abundance at age a subjected to both fishing and natural mortality instantaneously through the year. For the per recruit analysis, an arbitrary constant equal to 4,000 fish was set for N_r, where r = the age at first recruitment into the population (age 3 in this case). However, in reality recruitment is highly variable. The constant of 4,000 recruits (at age 3) was chosen because it generates a population of over 10,000 fish; the true pristine abundance at Florence Lake is unknown. Results of the 1991 to 1994 mark-recapture experiments at Florence Lake resulted in a population estimate of about 6,000 cutthroat trout over 180 mm. Since this analysis is considering trout age 3 (~150 mm) and above, the value of 10,000 fish was chosen as a round estimate of pristine abundance.

Female spawning abundance at age a, FSN_a, is defined as:

$$FSN_a = \chi_f m_a N_a, \tag{3.5}$$

where female spawning abundance is the product of the total abundance at age, the proportion mature at age, and the estimated proportion of females (χ_f) in the population. Egg production at age is the product of fecundity and female spawning abundance:

$$E_a = \tilde{f}_a FSN_a. \tag{3.6}$$

Total gonad volume at age is a product of gonad volume at age (Vg_a) and female spawning abundance:

$$GV_a = Vg_a FSN_a. \tag{3.7}$$

Estimates of life history parameters were established using data from chapter two and other independent methods and studies of coastal cutthroat trout.

Harding et al. (1999) presented the first unbiased estimate of annual survival for large (≥ 180 mm FL) lake resident cutthroat trout in Southeast Alaska (annual survival = 0.51, SE = 0.06). This estimate was established from mark-recapture experiments at Neck Lake, on the north end of Prince of Wales Island, which has a similar surface area and cutthroat trout length composition as Florence Lake. This survival corresponds to a total mortality rate (Z) of 0.67 and includes fishing mortality. Mortality from one sampling event to the next was estimated for cutthroat trout at Florence Lake during the 1991-1994 mark-recapture experiments. However, most of these estimates are undoubtedly biased due to fish movement into unsampled areas (spawning streams and deeper lake strata) (Rosenkranz et al. 1999). The Alverson-Carney (1975) approach to approximating natural mortality using the LVB parameter κ and the maximum observed age (estimated as age 15 in this case), was also examined. This method yielded a natural mortality estimate of M = 0.45.

Considering the factors above, an intermediate value for a natural mortality estimate of M = 0.5 was used in this study. Since sustained yield analysis of Southeast Alaska trout populations was robust to variations in natural mortality (Der Hovanisian 1994; Ericksen 1997), varying natural mortality estimates will not be examined. A natural mortality estimate much greater than 0.5 for Florence Lake simply would not generate the age structure observed.

Angler selectivity (s_a) is a logistic function variant on the minimum size limit:

$$s_a = 1/\left(1 + e^{-\gamma(x-[MSL-1])}\right), \tag{3.8}$$

where x is the average total length (cm) at age a, MSL is the minimum size limit in cm total length, and $\gamma = 1$; this value was chosen because it provided a realistic selectivity transition (not to steep or flat). One inch was subtracted from the MSL (corresponding to the inflection point) to account for those trout experiencing fishing mortality that are under the MSL.

With a MSL, it is not realistic to assume all fish over a certain length will be harvested if caught. Some fish, even though 2 to 3 inches under the MSL are still harvested (Sgt. Todd Sharp, Alaska Fish and Wildlife Protection, personal communications), and this should be taken into account when managing a trout fishery (Wright 1992). In addition, this selectivity function recognizes that many fish, including those just under the size limit, will fall victim to catch and release mortality from excessive handling.

With a 12-inch MSL, this logistic function estimates angler selectivity to be approximate 3% at 10 inches, 50% at 11 inches, and 93% at 12 inches. While this does present a worst-case scenario, it is unlikely that angler compliance will be 100% when many lakes are remote and presence of enforcement officers rare. With no MSL, all fish caught are assumed to be harvested.

Maturity, fecundity, growth, and population sex proportions were estimated in chapter two. The maturity relationship was converted from fork length to total length using the fork length to total length regression statistics estimated in chapter two. Since total length was also measured for all of the cutthroat trout sampled, the fecundity and growth parameters were estimated by refitting the data to the models incorporating the total length (instead of the fork length) measurements. For commonality with other studies, the LVB growth model (Schnute case 5) was used to estimate growth. In chapter two, Case 5 was found to have an RSS similar to that of Case 3 and was not significantly different from Case 1. The estimate of the population sex proportions was estimated from the pilot and main maturity studies.

The output obtained from this analysis is levels of fishing mortality corresponding to various biological reference points (BRP's). In response to different minimum size limits that are simulated by an adjusted angler selectivity, the levels of fishing mortality were compared in an effort to examine the effects of each on the population. To standardize the comparison, all fishing mortalities were calculated using the achievement of a certain BRP, such as $F_{40\%}$ (spawning biomass per recruit). However, for a recreational fishery, it is probably more important to preserve spawning abundance, and Quinn and Szarzi (1993) recommend preserving some percentage of the egg production or spawning abundance per recruit.

A conservative approach to regulation crafting would be to protect a certain percentage of female cutthroat trout, assuming enough mature males remain in the population to spawn with the females. Since males mature earlier and at a smaller size than females, a regulation based on females would by default also provide for adequate male spawners (Wright 1992, Ericksen 1997). Therefore, in the following analysis, BRP's associated with conserving some percentage of the pristine female spawning population and not strictly the population as a whole are used. In addition, I followed Quinn and Deriso's (1999) recommendation for preserving 45% to 60% of the unfished spawning abundance. The statistic $F_{N50\%}$ was also adopted by Der Hovanisian (1994) and Ericksen (2000). I thus adopt BRP's of $F_{N50\%}$ (female spawning abundance per recruit) and $F_{R40\%}$ (egg production per recruit) for this analysis. Comparatively, a third BRP will be calculated, $F_{GV45\%}$ (the fishing mortality which reduces the gonad volume per recruit to 45% of its unfished gonad volume per recruit). The percentage of 45 was chosen because it represents a mid-point between other two indices of spawning potential.

Length-based model

Quinn et al. (1998) presented an extension to the length-based model of Deriso and Parma (1988), in which stochastic growth is accounted for from one time period (a year) to the next by utilizing the LVB growth model parameters (Cohen and Fishman 1980). I modified the length-based population model to act as a basic per recruit analysis (a one time recruitment of 4000 fish at age 3), and added equations for maturity and fecundity to provide spawning abundance, spawning biomass, total egg production, and gonad volume.

Let

$N_a(x)$ = abundance at age a as a function of length x

M = natural mortality

$s_a(x)$ = angler selectivity at age a as a function of length x

$\tilde{f}(L)$= gross fecundity of a female at length L

$m(L)$ = proportion of mature females at length L

$Vg(L)$ = gonad volume of a mature female at length L

F = full recruitment fishing mortality

$F_a(x) = s_a(x)F$ = fishing mortality at age a as function of length x (3.9)

$Z_a(x) = M + F_a(x)$ = total instantaneous mortality as a function of length x. (3.10)

Starting at age r (age of recruitment set to age 3 as is in the age-based model), the length distribution of those individuals is:

$$N_r(x) = N_r f_r(x), \tag{3.11}$$

where the probability density function (PDF) for the length of fish at age r is:

$$f_r(x) \sim N_D(\mu_r, \sigma_r^2) = e^{-\frac{1}{2\sigma_r^2}(x-\mu_r)^2} / \xi_r. \tag{3.12}$$

This equations states that the distribution of lengths is discrete normal (N_D) with a mean of μ_r and variance of $\sigma^2{}_r$. The normalizing constant ξ_r ensures that the sum of the lengths in that

age r sum to one and has the form:

$$\xi_r = \sum_x e^{-\frac{1}{2\sigma_r^2}(x-\mu_r)^2}. \tag{3.13}$$

In what follows, a is the age of the recruits as they are followed through their life, experiencing both natural and fishing mortality. The number of individuals at length x after experiencing mortality (Z) is:

$$N_{a,Z}(x) = N_a\, p_{a,Z}(x), \tag{3.14}$$

where the distribution of lengths in the population after mortality is:

$$p_{a,Z}(x) = f_a(x) e^{-Za,x,}, \tag{3.15}$$

and the probability density function (PDF) for length after experiencing mortality is:

$$f_{a,Z}(x) = p_{a,Z}(x) / \sum_{x} p_{a,Z}(x). \tag{3.16}$$

For simplicity and consistency with the age-based analysis, growth will be explained with the von Bertalanffy (LVB) model. The LVB model with inclusion of stochastic error was first derived by Cohen and Fishman (1980) and later utilized by Deriso and Parma (1988) and Quinn et al. (1998).

The deterministic LVB equation is:

$$L_a = L_\infty(1 - e^{-\kappa(a-a_0)}), \tag{3.17}$$

where L_∞ is asymptotic length, κ is the LVB growth parameter, and a_0 is the age at which length = 0. Cohen and Fishman (1980) present the equivalent equation for the expected length at age a+1 for a fish of length x at age a:

$$\mu_{a+1}(x) = L_\infty(1 - \rho) + \rho x, \tag{3.18}$$

where ρ is the Brody coefficient: exp($-\kappa$). The associated variance is

$$\sigma_{a+1}^2 = \sigma^2 \frac{1 - \rho^{2(a+1-r)}}{1 - \rho^2} + \rho^{2(a+1-r)} \sigma_r^2. \tag{3.19}$$

At the beginning of age a+1, the relative distribution of lengths is

$$p_{a+1}(L) = \sum_x f_a(x) e^{-Z_{a,x}} e^{-\frac{1}{2\sigma_{a+1}^2}[L-\mu_{a+1}(x)]^2} / \xi_{a+1}. \qquad (3.20)$$

where ξ_{a+1} is a normalizing constant. This equation includes, relatively, the mortality equation (3.14) and the normal PDF for the length distribution after a one year growth increment (Quinn et al. 1998: 533–537).

The total population at age a+1 is equal to:

$$N_{a+1} = \sum_L N_{a+1}(L), \qquad (3.21)$$

where $N_{a+1}(L)$ is equal to the total population at length at age a+1 given by

$$N_{a+1}(L) = N_a p_{a+1}(L). \qquad (3.22)$$

Transformation of abundance to female spawning abundance, biomass, female spawning biomass, total egg production, and total gonad volume is achieved by the incorporation of the length-based weight, maturity, fecundity, sex proportion, and gonad volume relationships established in chapter two:

$$FSN_a = \sum_L SN_a(L)\chi_f = \sum_L N_a(L)m(L)\chi_f, \tag{3.23}$$

$$B_a = \sum_L B_a(L) = \sum_L N_a(L)W(L), \tag{3.24}$$

$$FSB_a = \sum_L FSN_a \chi_f, \tag{3.25}$$

$$E_a = \sum_L FSN_a(L)\tilde{f}(L). \tag{3.26}$$

$$GV_a = \sum_L FSN_a(L)V_g(L). \tag{3.27}$$

The selectivity, maturity, and fecundity equations as a function of length are analogous to those used for the age-based per recruit analysis. To standardize the use of these functions for the analysis, they were utilized as length-based functions based upon a length index for that same age class in the age-based method. The additional pieces of information needed for the length-based method are μ_r (mean length of recruits), σ^2_r (variance around the μ_r), and σ^2 (variance in annual growth). The mean length of the recruits was taken directly from the age and length data of age 3 fish from chapter 2. Using the Cohen and Fishman (1980) stochastic growth model, σ^2_r and σ^2 were estimated by fitting the predicted age and length distributions to those found in the maturity study.

The output attained from this analysis is directly comparable to that of the age-based method. Levels of F (fishing mortality) were estimated for the BRP's investigated, $F_{N50\%}$ (female spawning abundance), $F_{E40\%}$ (egg production), and $F_{GV45\%}$ (gonad volume).

RESULTS

Southeast Alaska trout MSL

The goal of the trout MSL in Southeast Alaska is to allow at least 60% of cutthroat an opportunity to spawn at least once before being susceptible to angler harvest. In chapter two, total length (inches) at maturity was estimated for both male and female cutthroat trout at Florence Lake (Figure 2.13). The proportions of mature male and female cutthroat trout at different 1-inch MSL intervals are displayed in Table 3.1. At the 12-inch MSL, 80.0% of the females and 89.5% of the males are mature. In 2001, the MSL was reduced to 11 inches, at which 78.4% of the female cutthroat trout and 78.5 % of the males are mature. With a 10-inch MSL in effect, these percentages drop to 67.8% for females and 60.9% for males; at 9 inches, the percentages are 32.3% for females and 40.0% males. Therefore, a 10-inch MSL is the minimum size necessary to allow a majority of males and females to spawn once (under perfect implemention with no hooking mortality).

Table 3.1. Proportion mature at different MSL's and per recruit analysis fishing mortality BRP's for coastal cutthroat trout at Florence Lake.

MSL (TL)	BRP expressed as fishing mortality rate (F)							
	Prop. Mature at MSL		Age-Based			Length-Based		
Inches	Males	Females	$F_{N50\%}$ [a]	$F_{E40\%}$ [b]	$F_{GV45\%}$ [c]	$F_{N50\%}$ [a]	$F_{E40\%}$ [b]	$F_{GV45\%}$ [c]
0	–	–	0.192	0.212	0.159	0.211	0.232	0.171
8	21.6%	5.7%	0.251	0.267	0.192	0.284	0.299	0.210
9	40.0%	32.3%	0.388	0.383	0.254	0.436	0.426	0.274
10	60.9%	67.8%	0.808	0.698	0.388	0.869	0.737	0.400
11	78.5%	78.4%	3.248	2.160	0.765	3.139	1.985	0.697
12	89.5%	80.0%	∞	∞	2.743	∞	∞	1.788

[a] reference fishing mortality that results in female spawning abundance 50% that of the unfished population.

[b] reference fishing mortality that results in egg production 40% that of the unfished population.

[c] reference fishing mortality that results in gonad volumes 45% that of the unfished population.

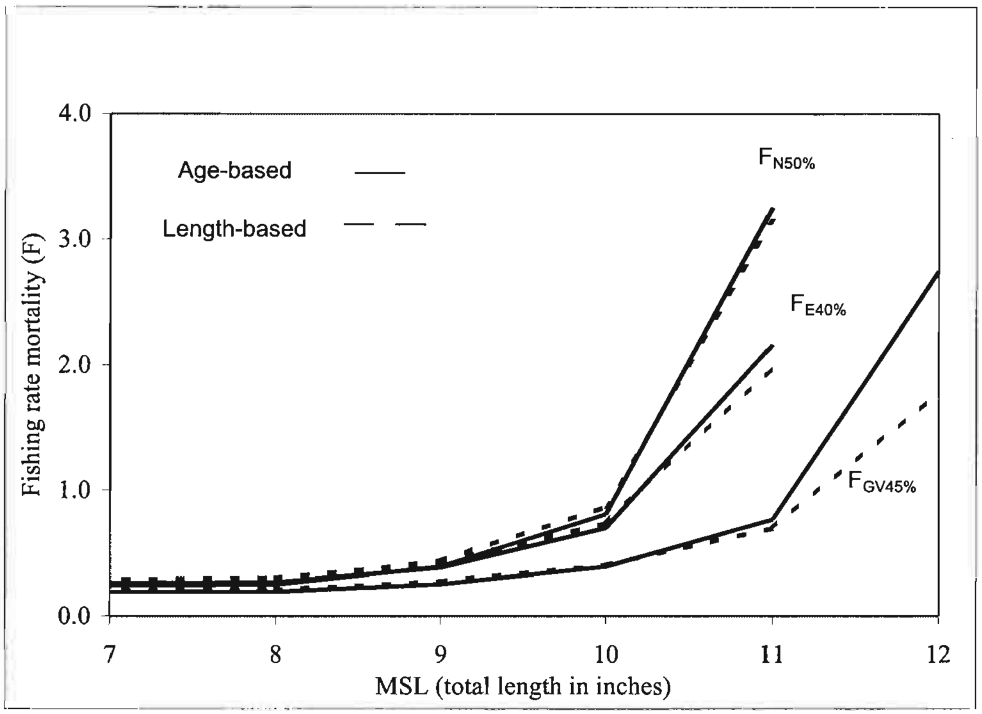


Figure 3.1. Graphical interpretation of the per recruit analysis fishing mortality BRP's at different MSL's for coastal cutthroat trout at Florence Lake.

Per recruit analysis

A summary table of per recruit analysis population parameter inputs is presented in Table 3.2. Minimum size limits have a profound effect on the level of fishing pressure needed to reduce the population to similar levels of reproductive potential. The reference fishing mortality rates for the BRP's $F_{N50\%}$ (female spawning abundance), $F_{E40\%}$ (egg production), and $F_{GV45\%}$ (total gonad volume), are displayed in Table 3.1 and graphically in Figure 3.1. The length-based per recruit analysis of these BRP's was comparable to the age-based analysis up to the 11-inch MSL. For no MSL up to a 10-inch MSL, the length-based estimates yielded rates of F that were, on average, 9% greater than those of the age-based method. Between the 10- and 11-inch MSL, the length-based estimates yielded rates of F that were, on average, 7% less than those of the age-based method; for the 12-inch MSL ($F_{GV45\%}$ only) the length-based estimate was 35% less than the age-based estimate. The length-based estimates of F are probably more accurate than age-based estimates, yet since the length-based estimates are larger, the age-based estimates likely are more conservative measures.

For no MSL and a 9-inch MSL, the $F_{E40\%}$ BRP yielded higher values of F than the $F_{N50\%}$ BRP, but for a 10 inch MSL and above, $F_{N50\%}$ yielded higher values of F. In other words, it took a higher rate of fishing pressure to decrease the egg production to 40% of its pristine state (per recruit) than to decrease the female spawning abundance to 50% of its pristine state, when the MSL is small or non existent. When the MSL is larger, more fishing pressure is required to decrease the female spawning abundance to 50% of its

Table 3.2. Per recruit analysis age-based and length-based parameter inputs.

Parameter or statistic	Value	Definition
L_∞	66.441	LVB growth model parameter L_∞.
κ	0.057	LVB growth model parameter κ.
σ^2	0.644	[a] Variance in annual growth.
μ_r	16.88	[a] Mean length of recruits (age 3).
σ_r	1.52	[a] Variance around μ_r.
M	0.5	Natural mortality.
χ_f	0.582	Population proportion of females.
$L_{50\%}$	20.32	[b] Selectivity parameter: length where 50% of the fish are vulnerable to angling pressure (MSL − 1 inch).
γ	1.00	Selectivity parameter: gamma.
α	0.004	Length/weight allometric parameter α.
β	3.203	Length/weight allometric parameter β.
α_f	0.057	Fecundity allometric parameter α.
β_f	2.569	Fecundity allometric parameter β.
m_∞	0.802	Female maturity/length logistic model parameter m_∞
κ_m	0.827	Female maturity/length logistic model parameter κ.
γ_m	23.411	Female maturity/length logistic model parameter γ.

Note: All estimates are based in centimeters total length.

[a] Used exclusively in length-based per recruit analysis.

[b] The minimum size limit (MSL) in inches total length was converted to cm.

pristine state than it does to decrease the egg production to 40% of its pristine state. This is because with a larger MSL, the more fecund, larger fish would be harvested and thus the egg production would fall more rapidly than the abundance.

Without exception, much lower levels of fishing pressure were required to reduce the total gonad volume of the spawning female cutthroat trout to 45% of its pristine state than to reduce the spawning abundance or egg production to similar levels (Table 3.1, Figure 3.1). With an 11-inch MSL, it takes very high fishing pressure to reduce to population to the $F_{N50\%}$ and $F_{E40\%}$ BRP's (averaging 2.6), but only relatively high fishing pressure (about 0.7 to 0.8) to reduce the population to the $F_{GV45\%}$ BRP.

Not only does the 12-inch MSL protect a high percentage of cutthroat trout at Florence Lake until they mature, but also this MSL resulted in a fishery in which it would almost be impossible to overfish the population (Table 3.1). This is because there are not many fish in Florence Lake over 12 inches. The 11-inch MSL, as well, represented a situation where the fishing pressure would have to be high in order to reduce the spawning abundance and egg production significantly. Between the 11 and 10-inch MSL, there is a large drop in fishing pressure necessary to reduce the reproductive potential to a certain level (for $F_{N50\%}$ and $F_{E40\%}$ BRP's); with an 11-inch MSL, those fish vulnerable to fishing at Florence Lake could receive 330% more fishing pressure than with a 10-inch MSL to affect the population similarly. Comparatively, for the $F_{GV45\%}$ BRP, the increase in fishing pressure allowed between the 10- and 11- inch MSL is only 40 to 50%.

Considering the actual differences between the age-and length- based analyses and the error present with each, there are no fundamental differences between the two up to the 11-inch MSL. However, differences are more pronounced at the 12-inch MSL, and therefore, I reject the null hypothesis that there will be no significant difference in the fishing mortality estimates of sustained yield for the age or the length based per recruit analyses. Tables B1 to B5 display examples of the comparison between per recruit analysis population statistics (e.g. abundance, female spawning population, gonad volume, and egg production by age) of length- and age-based methods for varying MSL's and rates of fishing pressure.

DISCUSSION

Florence Lake is the only non-stocked lake in Southeast Alaska that does not have a MSL regulation for the harvest of cutthroat trout because of its large population size (Table 1.2). The 12, 11, and 10-inch MSL's would protect a majority of the cutthroat until they have an opportunity to spawn. Considering all information, enough evidence exists to reject the null hypothesis that the goal of protecting 60% of cutthroat trout until they have a chance to spawn at least once will not be met for Florence Lake with a MSL of 11 inches. If the MSL was set at a level to protect 60% of the fish until they had an opportunity to spawn, it would be around 10 inches.

There is a caveat in this situation of comparing the proportion of the fish mature at the MSL to the goal of protecting fish until they can spawn. That is, maturity does not necessarily indicate having an opportunity to spawn (i.e., winter mortality may occur); thus, these results should be regarded cautiously. Since these lengths were sampled during October, and little growth would occur before spring spawning, the MSL values correctly reflect the size implications for the spawning population. The issue of skip spawning also has a bearing on a trout's opportunity to spawn; however, this reproductive trait is accounted for in the estimate of proportion mature.

For Florence Lake, the 10-inch MSL would be sufficient to protect a majority of cutthroat trout before maturity and the lake can tolerate considerable fishing pressure without dangerously limiting the reproductive capability of the population. However, a conservative regulation would protect a high percentage and be robust to fluctuations over time and to errors in estimation. Historically, before the Florence Lake watershed was logged, the lake received high fishing pressure. In 1979, Mills (1981) reported a cutthroat trout harvest of 1,727 fish at Florence Lake. Between 1984 and 1988, the harvest declined from 985 to 388 cutthroat per year (Jones et al. 1990). By assuming a population size similar to this study's analysis, the level of F for that range of harvest (and an angler selectivity equal to a 9-inch MSL) would be between 2.38 and 0.14, showing the possibility of overfishing. With increased fishing pressure (such as that before logging), a MSL would be a more necessary regulatory measure for the population. Another aspect to consider is that when the size limit falls below a certain acceptable threshold to anglers, there will be little difference in population length compositions between no MSL and a small MSL (Hunt 1970).

Ericksen (1997) estimated the effect that MSL's would have on the Florence Lake cutthroat population and also found that MSL's greatly influenced the analysis. There were some fundamental differences between Ericksen's (1997) study and this one: (1) Only an age-based per recruit analysis was done. (2) No information on maturity or fecundity was available, so the BRP's calculated were the fishing pressure needed to reduce the abundance and harvest of age 7+ cutthroat trout to 40% of the unfished population. (3) Natural mortality of M = 0.4 and M = 0.6 were used, not M = 0.5. (4) The angler selectivity logistic function (similar to the one in this study) assumed all fish below the MSL were voluntarily released without harm.

For comparison, I repeated my length-based per-recruit analysis without the maturity and fecundity data and a BRP $F_{N40\%}$ for abundance of age 7+ fish. My length-based per recruit estimate for the BRP was 0.46, compared to Ericksen's estimate of 1.04 at 9-inch MSL and M = 0.6. This difference is most likely due to the difference in the selectivity functions, growth parameters (results of aging), and to a small extent the natural mortality parameter. Coggins (1997) found ageing bias and precision to have strong effects on estimates of sustained yield. The selectivity function in this study allowed a certain amount of fishing mortality to occur below the size limit, unlike that of Ericksen. With a 10 inch MSL (selectivity 50% at nine inches; comparable to Ericksen) and M = 0.6, the estimate $F_{N40\%}$ from the length-based model rises to 1.09. Taking the selectivity and natural mortality differences into account shows both of these analyses to be comparable but illustrates the significance of determining the extent to which anglers harvest undersize fish.

The length-based and age-based per recruit analyses in this study performed adequately, and comparatively up to the 11-inch MSL BRP estimates. At the 12-inch MSL, there was a large difference in $F_{GV45\%}$ BRP estimates. Almost all differences between the age- and length-based methods are attributable to the values of σ^2 (variance in annual growth) and σ_r (variance of the recruits at age 3) estimates using the Cohen and Fishman (1980) stochastic growth model. These parameters supply randomness in size and length of fish at age, which is obviously more realistic than the age-based method that assumes all fish at age a are of a certain size and maturity level (based on the fish in the sample). With this inclusion of stochasticity the length-based method should yield more accurate results.

The length-based model is harder to construct and to modify, yet once developed, is as easy to use as the typical age-based method. The benefit of the length-based model is that the output will give length frequencies by age for the entire population. This kind of virtual population simulation will allow a fishery manager to fit these lengths to length at age in the harvest (sport or commercial) and to simultaneously estimate important population parameters (e.g. natural mortality) within the model with a simple solver routine.

Lower levels of fishing pressure were required to reduce the total gonad volume of the spawning female cutthroat trout to 45% of its pristine state than to reduce the spawning abundance or egg production to similar levels (Table 3.1, Figure 3.1). Without a quantitative measure of egg viability and survival of progeny from large eggs compared to small eggs, the success of the strategy to preserve a percentage of gonad volume cannot be measured.

I recommend that ADF&G management of cutthroat trout in Southeast Alaska be broadened to consider preservation of a percentage of gonad volume, because this measure produced the most conservative results and is based on the actual biological feature of increased gonad volume with size. From this study, the importance of the larger and more fecund fish is evident. Utilizing these per recruit analyses, and information collected from other lakes sampled for cutthroat trout maturity, will yield more information on the Southeast Alaska trout MSL's effect on region-wide harvests at various lakes.

The coastal cutthroat trout population in Southeast Alaska represents one of the last cutthroat stocks inhabiting much of its native range. There are literally hundreds of cutthroat trout streams and lakes in the region, each as unique and often isolated as the next. Yet, minimal fishing pressure can easily do long-term damage to this slow growing long-lived species. This resource is extremely important to both the ecosystems that they coexist with and to the recreational fisherman who enjoy catching native trout. It is my hope that this study lends knowledge that will help preserve the coastal cutthroat trout in its pure form.

LITERATURE CITED

Alaska Department of Fish and Game. 2003. Trout regulations in Southeast Alaska. http://www.sf.adfg.state.ak.us/statewide/regulations/2003/southeast/pdfs/trout.pdf

Alverson, D. L., and M. J. Carney. 1975. A graphic review of the growth and decay of population cohorts. J. Cons. Int. Explor. Mer 36:133-143.

Avery. E. L. 1985. Sexual maturity and fecundity of brown trout in central and northern Wisconsin streams. Technical Bulletin No. 154. Department of Natural Resources, Madison.

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout Salmo trutta L. J. Fish Biol. 1:349-353.

Behnke, R. J. 1992. Native trout of western North America. Amer. Fish. Soc. Monograph 6. Bethesda. 275p.

Behnke, R. J. 1997. Evolution, systematics, and structure of *Oncorhynchus clarki clarki*. In J. D. Hall, P. A. Bisson and R. E. Gresswell (editors), Sea-run cutthroat trout: Biology, mangement, and future conservation, p. 306. Oregon Chapter, American Fisheries Society, Corvallis.

Bryant, M. D., and S. J. McCurdy. 1995. The Margaret Lake Monitoring Program: Assessment of the resident cutthroat trout and Dolly Varden and introduced anadromous salmonids in Margaret Lake. Progress Report for 1995 to U. S. D. A. Forest Service, Ketchikan Ranger District. Pacific Northwest Research Station, Forestry Sciences Laboratory, Juneau, Alaska.

Bulkley, R. V. 1961. Fluctuations in age composition and growth rate of cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service. Research Report 54.

Bunag, D. M. 1956. Spawning habits of some Phillipine tuna based on diameter measurements of the ovarian ova. Phillipine Journal of Fisheries 4:145-175.

Burnham-Curtis, M. K., and C. R. Bronte. 1996. Otoliths reveal a diverse age structure for Humper lake trout in Lake Superior. Transactions of the American Fisheries Society 125:844-851.

Carlander, D. K. 1966. Relationship of limnological features to growth of fishes in lakes. Verh. Inter. Verein. Limnol. 16:1172-1175.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studies by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60.

Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48:734-750.

Clark, W.G. 1993. Groundfish exploitation rates based on life history parameters. In S. J. Smith, J. J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

Cohen, M. D., G. S. Fishman. 1980. Modeling growth-time and weight-length relationships in a single year-class fishery with examples on North Carolina pink and brown shrimp. Can. J. Fish. Aquat. Sci., Vol. 37:1000-1011.

Der Hovanisian, J. A. 1994. Stock assessment of rainbow trout in a Southeast Alaska impoundment. M.S. thesis, University of Alaska Fairbanks.

Dahl, Kn. 1917. Studies of trout and trout-waters in Norway. Fiskeriinsp. Indberetn. Kristiania, 1:107.

Deriso, R. B., and A. M. Parma. 1988. Dynamics of age and size for a stochastic population model. Can. J. Fish. Aquat. Sci., Vol. 45:1054-1068.

Downs, C. C., R. G. White, and B. B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout (*Oncorhynchus clarki lewisi*). North American Journal of Fisheries Management, Vol. 17:85-92.

Ericksen, R. P. 1997. Estimation of aging accuracy and precision, growth, and sustained yield of coastal cutthroat trout in Southeast Alaska. M.S. thesis, University of Alaska Fairbanks.

Ericksen, R. P. 1999. Scale aging manual for coastal cutthroat trout from Southeast Alaska. Alaska Department of Fish and Game, Special Publication No. 99-4, Anchorage.

Ericksen, R. P. 2000. Stock assessment of dolly varden in the Chilkoot Lake drainage, 1997-1998. Alaska Department of Fish and Game, Fishery Data Series No. 00-14, Anchorage.

Fuss, H. J. 1982. Age, growth and instream movement of Olympic Peninsula coastal cutthroat trout (*Salmo clarki clarki*). M.S. thesis, School of Fisheries, University of Washington, Seattle, 128.

Giger, R. D. 1972. Ecology and management of coastal cutthroat trout in Oregon. Oregon State Game Commission, Fishery Research Report Number 6, Corvallis.

Gresswell, R.E. and R.D. Harding. 1997. The role of special angling regulations in management of coastal cutthroat trout. In J.D. Hall, P.A. Bisson and R.E. Gresswel (eds.), Sea-run cutthroat trout: biology, management, and future conservation, pp. 151-156. Am. Fish. Soc., Corvallis.

Groot, C., and L. Margolis. Ed. 1991. Pacific salmon life histories. UBC press. Vancouver. 564p.

Hall, D. L. 1991. Growth, fecundity, and recruitment responses of stunted brook trout populations to density reduction. PhD thesis. The University of British Columbia.

Harding, R. D. 1994 Abundance and length composition of cutthroat trout in Florence, Turner, and Young lakes, Southeast Alaska, 1994. Alaska Department of Fish and Game, Fishery Data Series No. 95-43, Anchorage.

Harding, R. D., R. E. Chadwick, and G. M. Freeman. 1999. Abundance, length composition, and annual mortality of cutthroat trout at Neck Lake, Southeast Alaska, 1996 through 1998. Alaska Department of Fish and Game, Fishery Data Series No. 99-42. Anchorage.

Harding, R. D. 1999. Evaluation of short-term handling and tagging mortality of cutthroat trout at Florence Lake, Southeast Alaska. Alaska Department of Fish and Game, Fishery Data Series No. 99-24, Anchorage.

Hayashizaki, K., M. Hirohashi, and H. Ida. 1995. Effect of egg size on the characteristics of embryos and alevins of chum salmon. Fish. Sci. 61: 177-180.

Hoenig, J.M., M.J. Morgan, and C.A. Brown. 1995. Analysing differences between two age determination methods by tests of symmetry. Can. J. Fish. Aquat. Sci.52:364-368.

Hooton, B. 1997. Status of coastal cutthroat trout in Oregon. In J.D. Hall, P.A. Bisson and R. E. Gresswell (editors), Sea-run cutthroat trout: Biology, management, and future conservation, p. 57-67. American Fisheries Society, Corvallis.

Hunsaker, D., II, and L. F. Marnell. 1970. Hooking mortality of lure-caught cutthroat trout (*Salmo clarki*) in relation to water temperature, fatigue, and reproductive maturity of released fish. Transactions of the American Fisheries Society 99:684-688.

Hunt, R. L. 1970. A compendium of research on angling regulations for brook trout conducted at Lawrence Creek, Wisconsin. Wisconsin Department of Natural Resources. Research Report 54, Madison.

Ishida, R., K. Takagi, and S. Arita. 1961. Criteria for the discrimination of mature and immature forms of chum and sockeye salmon in northern areas. Int. North Pac. Fish. Comm. Bull. 5:23-40.

Jones, D. E. 1976. Steelhead and sea-run cutthroat trout life in Southeast Alaska. ADF&G, Federal Aid in Fish Restoration, Annual Report of Progress, 1975-76, Project AFS-42, Volume 17 (AFS-42-4-B), Juneau.

Jones, D. E. 1978. Development and techniques for enhancement and management of cutthroat trout in Southeast Alaska. ADF&G, Federal Aid in Fish Restoration, Annual Report of Progress, 1977-178, Project AFS-42, Volume 19 (AFS-42-6-B), Juneau.

Jones, D. E. 1980. Development and techniques for enhancement and management of cutthroat trout in Southeast Alaska. ADF&G, Federal Aid in Fish Restoration, Annual Report of Progress, 1979-80, Project AFS-42, Volume 21 (AFS-42-8-B), Juneau.

Jones, D. E. 1981. Development and techniques for enhancement and management of cutthroat trout in Southeast Alaska. ADF&G, Federal Aid in Fish Restoration, Annual Report of Progress, 1979-80, Volume 22, Project (AFS-42-9-B), Juneau.

Jones, D. E. 1982. Development and techniques for enhancement and management of cutthroat trout in Southeast Alaska. ADF&G, Federal Aid in Fish Restoration, Annual Report of Progress, 1976-1982, Volume 23, Project (AFS-42-10-B), Juneau.

Jones, J. D. 1995. Southeast Alaska recreational cabin survey, 1994. Alaska Department of Fish and Game, Fishery Data Series No. 95-32, Anchorage, AK.

Jones, J. D., A. E. Bingham, and R. Harding. 1989. Cutthroat trout studies: Turner/Florence lakes, Alaska, during 1988. Alaska Department of Fish and Game, Fishery Data Series No. 111, Juneau, Alaska, USA.

Jones, J. D., R. Harding, and A. E. Bingham. 1990. Cutthroat trout studies: Turner/Florence lakes, Alaska, During 1989. Alaska Department of Fish and Game, Fishery Data Series No. 90-24, Anchorage.

Jones, J. D., and C. L. Seifert. 1997. Distribution of mature sea-run cutthroat trout overwintering in Auke Lake and Lake Eva in Southeastern Alaska. In J.D. Hall, P.A.

Bisson and R. E. Gresswell (editors), Sea-run cutthroat trout: Biology, management, and future conservation, p. 27-28. American Fisheries Society, Corvallis.

Jonsson, B., K. Hindar., and T. G. Northcote. 1984. Optimal age at sexual maturity of sympatric and experimentally allopatric cutthroat trout and dolly varden charr. Oecologia (Berlin) 61:319-325.

Johnston, J. M., and S. P. Mercer. 1976. Sea-run cutthroat trout in saltwater pens: broodstock development and extended juvenile rearing (with a life history compendium). Wash. State Game Dep. Fish. Res. Rep. AFS-57-1. 92 pp.

Kruse, C. G., W. A. Hubert., and F. J. Rahel. 1997. Using otoliths and scales to describe age and growth of Yellowstone cutthroat trout in a high-elevation stream system, Wyoming. Northwest Science 71:30-38.

Leeuw, A. D. 1987. Observations on cutthroat trout of the mosquito lake system Queen Charlotte Islands. B.C. Ministry of Environment, Skeena Fisheries Report #57, Smithers, B.C.

Mills, M. 1981. Statewide harvest study – 1979 data. Alaska Department of Fish and Game, Federal Aid in Fish Restoration and Anadromous Fish Studies, Annual Performance Report 1980-1981, Project F – 9 – 13, Volume 22 (SW-I-A), Juneau, Alaska, USA. 78p.

Mills, M. J., A. L. Howe., G. Fidler., and A. E. Bingham. 1996. Harvest, catch, and participation in Alaska sport fisheries during 1995. Alaska Department of Fish and Game, Anchorage. 212p.

Moring, J. R., K. J. Anderson, and R. L. Youker. 1981. High incidence of scale regeneration by potamodromous coastal cutthroat trout: Analytical implications. Transactions of the American Fisheries Society 123:358-367.

Morrow, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company. Anchorage. 248p.

Northcote, T. G. 1997. Why sea-run? An exploration into the migratory/residency spectrum of coastal cutthroat trout. In J.D. Hall, P.A. Bisson and R. E. Gresswell (editors), Sea-run cutthroat trout: Biology, management, and future conservation, p. 20-26. American Fisheries Society, Corvallis.

Pierce, B. E. 1984. The trouts of Lake Crescent, Washington. M.S. Thesis. Colorado State University, Fort Collins.

Pauley, G. B., and G. L. Thomas. 1993. Mortality of anadromous coastal cutthroat trout caught with artificial lures and natural bait. North American Journal of Fisheries Management 13:337-345.

Quinn, T. J., II, and N. J. Szarzi. 1993. Determination of sustained yield in Alaska's recreational fisheries. Proceeding of the international symposium on management strategies for exploited fish populations. Alaska Sea Grant College Program Report No. 93-02:61-84.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York. 480p.

Quinn II, T. J., C. T. Turnbull, and C. Fu. 1998. A length-based population model for hard-to-age invertebrate populations. In: F. Funk et al. (eds.), Fishery Stock Assessment Models. University of Alaska Sea Grant, AK-SG-98-01, Fairbanks, pp. 531-556.

Rosenkranz, G. E., R. P. Marshall, and R. H. Harding. 1999. Estimating natural mortality and abundance of potamodromous, lake dwelling cutthroat trout of Florence Lake, Alaska. Alaska Department of Fish and Game, Division of Sport Fish. Juneau.

Schmidt, A. E. 1997a. Southeast Alaska trout and steelhead management. Report to the Alaska Board of Fisheries. Alaska Department of Fish and Game, Division of Sportfish. Douglas.

Schmidt, A. E. 1997b. Status of sea-run cutthroat trout stocks in Alaska. In J. D. Hall, P. A. Bisson and R. E. Gresswell (editors), Sea-run cutthroat trout: Biology, management, and future conservation, pp. 80-86. American Fisheries Society, Corvallis.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci., Vol. 38:1128-1140.

Shepherd, G. R., and J. S. Idoine. 1993. Length-based analyses of yield and spawning biomass per recruit for black sea bass Centropristis striata, a protogynous hermaphrodite. Fishery Bulletin, U.S. 91:328-337.

Seber, G. A. F. 1982. The estimation of animal abundance, 2nd ed., Griffin, London. 654 p.

Taylor, M. J., and K. R. White. 1992. A meta-analysis of hooking mortality of nonanadromous trout. North American Journal of Fisheries Management 12:760-767.

Thompson, S. K. 1992. Sampling. John Wiley & Sons Inc. New York. 343p.

Thurow, R. F., C. E. Corsi, and V. K. Moore. 1988. Status, ecology, and management of Yellowstone cutthroat trout in the upper Snake River drainage, Idaho. Amer. Fish. Soc. Symposium 4:25-36.

Tomasson, T. 1978. Age and growth of cutthroat trout, *Salmo clarki clarki Richardson*, in the Rogue River, Oregon. M.S. Thesis. Oregon State University, Corvallis, 75 p.

Trippel. E. A., and H. H. Harvey. 1991. Comparisons of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci., Vol. 48:1446-1459.

Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. BioScience 45:759-771.

Trotter, P. C. 1987. Cutthroat: Native trout of the west. Colorado Assoc. Univ. Press. Boulder. 219p.

Trotter, P. C. 1989. Coastal cutthroat trout: A life history compendium. Transactions of the American Fisheries Society 118:463-473.

Trotter, P. C. 1997. Sea-run cutthroat trout: Life history profile. In J. D. Hall, P. A. Bisson and R. E. Gresswell (editors), Sea-run cutthroat trout: Biology, management, and future conservation, p. 7-15. American Fisheries Society, Corvallis.

West, C. J., and J. C. Mason. 1987. Evaluation of sockeye salmon (*Onchorhynchus nerka*) production from the Babine Lake development project. In: H. D. Smith, L.

Margolis, and C. C. Wood (editors). Sockeye Salmon (*Onchorhynchus nerka*) Population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96

Volodin, V. M. 1981. The effect of temperature on resorption in practically mature eggs and the development of the next generation of oocytes in the Blue Bream, *Abramis ballerus*, from Rybinsk Reservoir. Journal of Ichthyology 20(1):56-61.

West, G. 1990. Methods of assessing ovarian development in fishes: A review. Aust. J. Mar. Freshwater Res. 41:199-222.

Wright, S. 1992. Guidelines for selecting regulations to manage open-access fisheries for natural populations of anadromous and resident trout in stream habitats. North American Journal of Fisheries Management 12:517-527.

Yanusz, R. J. 1997. Status of sea-run cutthroat trout, sea-run dolly varden, and steelhead populations at Sitkoh Creek, Southeast Alaska, during 1996. Alaska Department of Fish and Game. Fishery Data Series No. 97-23. Anchorage.

Zar, J. H. 1974. Biostatistical analysis. Prentice Hall, Inc. Englewood Cliffs. 620p.

APPENDICES

Table A.1. Data compilation of cutthroat trout maturity information collected during the October 1997 study at Florence Lake, Southeast Alaska.

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
134	142	23.3	Female	Immature	0.02	0.00086	--	--
140	147	27.2	Female	Immature	0.03	0.0011	--	--
141	149	28.5	Male	Immature	--	--	--	--
143	151	29.2	Male	Immature	--	--	--	--
145	153	32.2	Male	Immature	--	--	--	--
149	157	31.6	Male	Immature	--	--	--	--
151	159	33.3	Female	Immature	0.06	0.0018	--	--
152	162	33.9	Male	Immature	--	--	--	--
156	166	37.1	Male	Immature	--	--	--	--
158	166	43.0	Female	Immature	0.07	0.00163	--	--
158	167	40.4	Male	Immature	--	--	--	--
162	171	41.5	Female	Immature	0.07	0.00169	--	--
162	171	43.8	Female	Immature	0.08	0.00183	--	--
162	173	42.1	Female	Immature	0.12	0.00285	--	--
165	176	47.1	Male	Immature	--	--	--	--
168	178	47.7	Male	Immature	--	--	--	--
169	178	48.2	Female	Immature	0.21	0.00436	--	--
172	181	51.6	Female	Immature	0.08	0.00155	--	--
172	182	49.9	Female	Immature	0.17	0.00341	--	--
173	182	50.9	Male	Immature	--	--	--	--
174	183	52.8	Male	Immature	--	--	--	--
174	183	51.2	Male	Mature	--	--	--	--
175	184	54.2	Female	Immature	0.36	0.00664	--	--
176	185	56.2	Female	Immature	0.05	0.00089	--	--
176	187	52.8	Male	Immature	--	--	--	--
178	187	54.4	Female	Immature	0.21	0.00386	--	--
178	187	52.0	Male	Immature	--	--	--	--
179	189	57.8	Female	Immature	0.13	0.00225	--	--
179	190	54.7	Male	Immature	--	--	--	--
179	188	58.7	Male	Immature	--	--	--	--
179	186	54.4	Male	Mature	--	--	--	--
182	193	58.3	Male	Immature	--	--	--	--
184	195	63.8	Female	Immature	0.19	0.00298	--	--
184	195	60.1	Male	Immature	--	--	--	--
185	196	59.4	Male	Immature	--	--	--	--
186	197	63.5	Female	Immature	0.1	0.00157	--	--
186	196	62.8	Female	Immature	0.17	0.00271	--	--

-continued-

Table A.1. (page 2 of 7)

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
186	197	57.5	Male	Immature	--	--	--	--
187	196	66.9	Female	Immature	0.25	0.00374	--	--
187	197	67.9	Male	Immature	--	--	--	--
188	197	60.1	Female	Immature	0.21	0.00349	--	--
189	199	64.3	Female	Immature	0.18	0.0028	--	--
190	201	68.3	Male	Immature	--	--	--	--
191	202	63.4	Male	Immature	--	--	--	--
192	202	66.8	Male	Immature	--	--	--	--
194	205	61.7	Female	Immature	0.04	0.00065	--	--
194	204	71.8	Female	Immature	0.17	0.00237	--	--
194	205	67.7	Male	Immature	--	--	--	--
194	203	65.2	Male	Immature	--	--	--	--
195	205	68.3	Female	Immature	0.14	0.00205	--	--
196	205	70.3	Male	Immature	--	--	--	--
196	206	68.7	Male	Immature	--	--	--	--
198	207	74.4	Female	Immature	0.15	0.00202	--	--
198	209	66.7	Male	Immature	--	--	--	--
198	207	76.7	Male	Mature	--	--	--	--
199	209	72.8	Female	Immature	0.11	0.00151	--	--
200	209	77.7	Male	Mature	--	--	--	--
201	213	73.2	Female	Immature	0.1	0.00137	--	--
202	211	79.4	Female	Immature	1.27	0.01599	--	1.95
202	211	73.7	Male	Mature	--	--	--	--
203	214	88.8	Female	Immature	0.18	0.00203	--	--
205	216	87.9	Female	Immature	0.19	0.00216	--	--
205	215	80.5	Female	Immature	0.21	0.00261	--	--
205	216	65.4	Female	Immature	0.63	0.00963	--	--
206	216	94.0	Male	Mature	--	--	--	--
207	215	87.9	Female	Immature	0.15	0.00171	--	--
207	218	77.5	Female	Immature	0.14	0.00181	--	--
207	217	80.3	Male	Immature	--	--	--	--
208	219	97.9	Female	Mature	4.14	0.04229	187	3.22
210	216	107.4	Female	Mature	3.8	0.03538	166	3.17
210	219	91.2	Male	Mature	--	--	--	--
212	223	94.4	Male	Immature	--	--	--	--
212	223	96.8	Male	Mature	--	--	--	--
214	226	87.0	Female	Immature	0.2	0.0023	--	--
214	226	95.3	Male	Immature	--	--	--	--
215	227	99.0	Female	Immature	0.12	0.00121	--	--

-continued-

Table A.1. (page 3 of 7)

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
215	228	99.7	Female	Immature	0.14	0.0014	--	--
215	229	101.8	Female	Immature	0.23	0.00226	--	--
215	226	99.2	Male	Immature	--	--	--	--
215	224	101.9	Male	Mature	--	--	--	--
216	226	101.5	Female	Immature	0.08	0.00079	--	--
217	227	102.9	Male	Immature	--	--	--	--
217	231	92.5	Male	Immature	--	--	--	--
217	228	99.2	Male	Mature	--	--	--	--
218	229	104.0	Female	Immature	0.21	0.00202	--	--
218	228	106.5	Female	Mature	3.58	0.03362	167	3.14
218	229	105.4	Male	Immature	--	--	--	--
220	232	104.8	Female	Immature	0.17	0.00162	--	--
220	231	109.2	Female	Mature	4.03	0.0369	186	3.22
222	231	106.6	Female	Immature	0.23	0.00216	--	--
222	230	103.3	Female	Mature	2.92	0.02827	132	3.10
223	235	116.7	Male	Immature	--	--	--	--
224	235	107.1	Female	Immature	0.21	0.00196	--	--
225	235	108.9	Female	Mature	3.29	0.03021	233	2.81
225	234	111.3	Female	Mature	5.33	0.04789	213	3.41
225	234	119.6	Male	Mature	--	--	--	--
226	235	103.7	Female	Immature	0.4	0.00386	--	--
226	236	115.6	Female	Mature	4.55	0.03936	262	3.06
227	239	112.6	Male	Immature	--	--	--	--
229	240	107.3	Female	Immature	0.2	0.00186	--	--
229	238	123.5	Female	Mature	2.98	0.02413	249	2.75
230	240	102.8	Female	Immature	0.48	0.00467	--	--
230	240	123.9	Female	Mature	3.91	0.03156	248	2.84
230	242	106.1	Male	Immature	--	--	--	--
230	241	117.8	Male	Immature	--	--	--	--
232	243	112.1	Female	Immature	0.1	0.00089	--	--
232	243	118.8	Female	Immature	0.2	0.00168	--	--
232	241	117.6	Female	Immature	0.21	0.00179	--	--
232	244	115.4	Female	Immature	0.25	0.00217	--	--
232	243	112.4	Female	Mature	2.96	0.02633	175	2.88
232	241	122.6	Female	Mature	5.12	0.04176	209	3.40
232	241	118.7	Male	Immature	--	--	--	--
232	243	114.8	Male	Immature	--	--	--	--
232	243	110.9	Male	Mature	--	--	--	--
233	244	119.4	Male	Mature	--	--	--	--

-continued-

Table A.1. (page 4 of 7)

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
233	243	114.8	Male	Mature	--	--	--	--
234	245	130.2	Female	Immature	0.9	0.00691	--	--
235	246	152.6	Female	Mature	6.39	0.04187	322	--
236	247	121.8	Female	Immature	0.22	0.00181	--	--
236	248	124.9	Female	Mature	4.82	0.03859	226	--
236	248	128.3	Female	Mature	5.52	0.04302	245	--
236	249	113.6	Male	Immature	--	--	--	--
237	246	131.7	Female	Mature	5.51	0.04184	206	--
238	251	129.6	Female	Immature	0.27	0.00208	--	--
238	248	119.3	Female	Mature	3.5	0.02934	160	3.05
238	247	126.0	Female	Mature	6.75	0.05357	205	--
238	249	119.3	Male	Immature	--	--	--	--
238	249	132.4	Male	Mature	--	--	--	--
239	250	132.7	Female	Immature	0.29	0.00219	--	--
239	248	133.8	Male	Mature	--	--	--	--
240	250	122.2	Female	Mature	4.81	0.03936	198	3.25
240	252	132.3	Male	Immature	--	--	--	--
241	253	150.4	Female	Mature	7.38	0.04907	245	3.53
242	252	139.9	Female	Mature	5.01	0.03581	193	3.16
244	254	142.8	Female	Mature	2.58	0.01807	278	2.45
244	254	138.7	Female	Mature	4.47	0.03223	159	--
244	253	156.8	Female	Mature	5.45	0.03476	200	3.44
244	255	141.1	Male	Mature	--	--	--	--
244	256	139.9	Male	Mature	--	--	--	--
245	257	134.1	Female	Mature	4.8	0.03579	226	3.13
246	257	147.0	Female	Immature	0.29	0.00197	--	--
246	257	138.7	Female	Immature	0.28	0.00202	--	--
246	257	139.3	Female	Mature	6.56	0.04709	280	--
248	259	157.6	Male	Immature	--	--	--	--
249	260	155.4	Female	Immature	0.33	0.00212	--	--
249	258	145.6	Male	Mature	--	--	--	--
250	263	152.7	Female	Mature	4.77	0.03124	194	--
251	263	151.5	Female	Immature	0.18	0.00119	--	--
251	260	155.5	Female	Mature	6.39	0.04109	260	3.39
251	262	154.5	Male	Mature	--	--	--	--
254	265	153.1	Female	Immature	0.65	0.00425	--	--
254	263	160.8	Female	Mature	6.43	0.03999	263	3.43
254	263	169.1	Female	Mature	7.23	0.04276	275	3.41
255	267	147.7	Female	Immature	0.27	0.00183	--	--

-continued-

Table A.1. (page 5 of 7)

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
255	265	130.8	Female	Immature	0.39	0.00298	--	--
255	265	168.9	Female	Mature	6.8	0.04026	261	--
255	264	166.0	Female	Mature	7.65	0.04608	276	--
255	264	164.9	Female	Mature	8.31	0.05039	296	3.53
255	267	169.0	Male	Mature	--	--	--	--
256	266	184.0	Female	Mature	9.69	0.05266	235	3.94
257	269	159.6	Female	Immature	0.29	0.00182	--	--
257	268	164.9	Female	Mature	7.83	0.04748	259	--
257	266	167.4	Male	Mature	--	--	--	--
259	273	164.7	Female	Mature	3.87	0.0235	212	--
259	271	166.2	Female	Mature	5.59	0.03363	248	3.24
259	269	153.7	Female	Mature	5.65	0.03676	208	--
259	270	159.3	Female	Mature	8.54	0.05361	290	3.58
259	270	163.2	Male	Mature	--	--	--	--
259	270	165.0	Male	Mature	--	--	--	--
260	269	181.6	Male	Mature	--	--	--	--
261	272	172.5	Female	Mature	6.75	0.03913	258	--
261	272	178.0	Female	Mature	8.86	0.04978	334	--
262	275	167.0	Female	Mature	6.6	0.03952	302	3.27
263	276	172.3	Female	Immature	0.44	0.00255	--	--
263	275	173.7	Male	Mature	--	--	--	--
265	278	187.8	Female	Mature	6.6	0.03514	274	--
265	276	170.1	Male	Mature	--	--	--	--
266	278	188.3	Male	Immature	--	--	--	--
266	277	181.8	Male	Mature	--	--	--	--
267	280	178.2	Male	Immature	--	--	--	--
267	278	201.5	Male	Mature	--	--	--	--
268	279	191.2	Female	Mature	6.13	0.03206	239	3.42
268	280	191.0	Female	Mature	7.78	0.04073	304	--
268	280	187.9	Female	Mature	7.84	0.04172	300	--
268	281	184.3	Female	Mature	9.45	0.05128	228	4.10
269	280	178.7	Female	Immature	0.3	0.00168	--	--
269	286	208.9	Female	Immature	0.44	0.00211	--	--
269	278	163.3	Female	Mature	5.03	0.0308	195	3.37
271	283	169.0	Female	Immature	0.34	0.00201	--	--
271	282	192.8	Female	Mature	7.11	0.03688	266	3.36
271	283	187.3	Male	Mature	--	--	--	--
272	281	184.6	Male	Immature	--	--	--	--
272	283	170.2	Male	Immature	--	--	--	--

-continued-

Table A.1. (page 6 of 7)

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
272	281	185.7	Male	Mature	--	--	--	--
272	282	188.4	Male	Mature	--	--	--	--
273	282	193.0	Female	Mature	7.25	0.03756	413	2.97
273	283	200.8	Male	Mature	--	--	--	--
274	285	169.8	Female	Mature	6.86	0.0404	239	--
274	283	196.6	Female	Mature	9.19	0.04674	301	3.63
274	285	201.9	Female	Mature	10.31	0.05106	330	3.68
274	288	204.0	Male	Immature	--	--	--	--
275	287	191.0	Female	Mature	7.95	0.04162	261	3.60
276	289	206.0	Male	Mature	--	--	--	--
279	290	216.3	Male	Mature	--	--	--	--
279	291	179.7	Male	Mature	--	--	--	--
281	293	226.9	Female	Immature	0.45	0.00198	--	--
281	294	188.2	Female	Mature	5.98	0.03177	280	3.19
281	291	204.2	Male	Mature	--	--	--	--
282	296	233.0	Male	Mature	--	--	--	--
283	294	229.4	Male	Mature	--	--	--	--
284	295	262.0	Female	Mature	13.45	0.05134	360	3.83
285	294	215.5	Female	Mature	11.52	0.05346	316	3.73
287	299	244.0	Female	Mature	11.23	0.04602	342	3.73
293	300	205.2	Female	Mature	6.68	0.03255	303	3.10
295	304	219.9	Female	Immature	0.65	0.00296	--	--
295	306	259.0	Female	Mature	14.9	0.05753	455	3.69
299	308	281.7	Male	Mature	--	--	--	--
300	310	253.0	Female	Mature	14.62	0.05779	490	3.58
301	312	264.0	Female	Mature	17.8	0.06742	413	4.10
303	314	268.9	Female	Mature	12.31	0.04578	495	3.47
303	314	275.0	Male	Mature	--	--	--	--
304	314	326.0	Female	Immature	1.09	0.00334	--	--
306	322	273.4	Female	Immature	0.55	0.00201	--	--
312	325	333.7	Male	Mature	--	--	--	--
314	323	308.0	Male	Mature	--	--	--	--
316	329	305.6	Female	Mature	16.73	0.05474	575	3.59
322	333	331.2	Male	Mature	--	--	--	--
332	345	390.0	Female	Mature	21.86	0.05605	548	3.78
332	334	375.0	Female	Mature	25.72	0.06859	569	4.15
337	348	356.0	Female	Mature	19.72	0.05539	464	4.03
340	352	360.6	Male	Mature	--	--	--	--
342	354	383.2	Female	Mature	13.22	0.0345	622	3.13

-continued-

Table A.1. (page 7 of 7)

Fork length (mm)	Total length (mm)	Weight (g)	Sex	Maturity	Ovary weight (g)	GSI	Fecundity	Average diameter of ova (mm)
346	360	424.1	Female	Mature	24.1	0.05683	473	4.25
346	358	440.0	Female	Mature	26.59	0.06043	707	3.94
349	352	391.0	Male	Mature	--	--	--	--
365	371	491.0	Female	Mature	29.57	0.06022	564	4.37
374	387	536.0	Male	Mature	--	--	--	--

Table A.2. Fecundity, length, average ova diameter, and variance statistics of cutthroat trout at Florence Lake, Southeast Alaska.

Fecundity N	Fork length in mm	Average diameter of ova n=30	s^2	Standard deviation	Estimated standard error
187	208	3.22	0.019	0.138	0.023
166	210	3.17	0.014	0.118	0.020
167	218	3.14	0.012	0.111	0.018
186	220	3.22	0.009	0.093	0.016
132	222	3.10	0.016	0.128	0.020
213	225	3.41	0.011	0.106	0.018
233	225	2.81	0.011	0.106	0.018
262	226	3.06	0.009	0.097	0.017
249	229	2.75	0.032	0.179	0.031
248	230	2.84	0.019	0.138	0.024
209	232	3.40	0.020	0.141	0.024
175	232	2.88	0.010	0.101	0.017
160	238	3.05	0.021	0.144	0.024
198	240	3.25	0.013	0.116	0.020
245	241	3.53	0.032	0.179	0.031
193	242	3.16	0.012	0.108	0.018
200	244	3.44	0.010	0.100	0.017
278	244	2.45	0.026	0.162	0.028
226	245	3.13	0.031	0.177	0.030
260	251	3.39	0.012	0.109	0.019
263	254	3.43	0.011	0.103	0.018
275	254	3.41	0.016	0.125	0.022
296	255	3.53	0.009	0.093	0.016
235	256	3.94	0.032	0.179	0.030
290	259	3.58	0.022	0.149	0.026
248	259	3.24	0.014	0.119	0.020
302	262	3.27	0.015	0.121	0.021
239	268	3.42	0.012	0.111	0.019
228	268	4.10	0.022	0.149	0.025
195	269	3.37	0.041	0.203	0.034
266	271	3.36	0.014	0.118	0.020
413	273	2.97	0.010	0.102	0.018
301	274	3.63	0.014	0.118	0.020
330	274	3.68	0.013	0.113	0.020
261	275	3.60	0.015	0.121	0.021
280	281	3.19	0.012	0.110	0.019
360	284	3.83	0.019	0.138	0.024

-continued-

Table A.2. (page 2 of 2)

Fecundity N	Fork length in mm	Average diameter of ova n=30	s^2	Standard deviation	Estimated standard error
316	285	3.73	0.021	0.146	0.025
342	287	3.73	0.013	0.114	0.020
303	293	3.10	0.015	0.124	0.022
455	295	3.69	0.021	0.144	0.025
490	300	3.58	0.019	0.138	0.024
413	301	4.10	0.015	0.124	0.022
495	303	3.47	0.016	0.126	0.022
575	316	3.59	0.010	0.101	0.018
569	332	4.15	0.018	0.135	0.024
548	332	3.78	0.018	0.133	0.024
464	337	4.03	0.012	0.111	0.020
622	342	3.13	0.057	0.239	0.043
707	346	3.94	0.013	0.113	0.020
473	346	4.25	0.030	0.172	0.030
564	365	4.37	0.016	0.125	0.022

Table A.3. Schnute growth model parameter estimates, standard error, RSS, and F-tests for fits of female cutthroat trout at Florence Lake.

	Additive									
	Case 1		Case 2		Case 3		Case 4		Case 5	
Parameter	Est.	se	Est.	se	Est.	se	Est.	se	Est.	se
y_1	158.39	6.44	160.51	4.45	158.48	5.16	176.25	2.70	159.15	4.73
y_2	340.86	8.35	338.94	7.30	340.75	6.62	363.23	5.92	340.09	7.11
κ	-0.01	0.31	0.14	0.03	0.00	0.00	0.00	0.00	0.05	0.03
γ	1.58	3.24	0.00	0.00	1.50	0.33	0.00	0.00	1.00	0.00
RSS	43,259		43,327		43,260		50,066		43,269	
$\hat{\sigma}$	17.90		17.85		17.83		19.12		17.84	
n	139		139		139		139		139	
df	135		136		136		137		136	

F-tests			F	P	F	P	F	P	F	P
vs Case 1			0.212	0.646	0.001	0.982	10.620	0.000	0.031	0.861
vs Case 2							21.151	0.000		
vs Case 3							21.397	0.000		
vs Case 5							21.362	0.000		

	Multiplicative									
	Case 1		Case 2		Case 3		Case 4		Case 5	
Parameter	Est.	se	Est.	se	Est.	se	Est.	se	Est.	se
y_1	156.70	4.07	158.82	3.40	157.35	3.72	171.02	2.47	157.92	3.51
y_2	341.44	11.21	335.24	9.07	338.44	7.92	374.53	7.35	337.41	8.82
κ	-0.11	0.28	0.15	0.03	0.00	0.00	0.00	0.00	0.06	0.03
γ	2.63	2.81	0.00	0.00	1.58	0.33	0.00	0.00	1.00	0.00
RSS	0.747		0.752		0.748		0.880		0.749	
$\hat{\sigma}$	0.0744		0.0744		0.0742		0.0802		0.0742	
n	139		139		139		139		139	
df	135		136		136		137		136	

F-tests			F	P	F	P	F	P	F	P
vs Case 1			0.864	0.354	0.143	0.706	12.007	0.000	0.340	0.561
vs Case 2							23.174	0.000		
vs Case 3							24.023	0.000		
vs Case 5							23.791	0.000		

Note: Shaded boxes denote parameters set at a specified number (e.g., 0.0 or 1.0).

Table A.4. Schnute growth model parameter estimates, standard error, RSS, and F-tests for fits of male cutthroat trout at Florence Lake.

	Additive									
	Case 1		Case 2		Case 3		Case 4		Case 5	
Parameter	Est.	se	Est.	se	Est.	se	Est.	se	Est.	se
y_1	161.13	4.71	163.48	3.99	161.92	4.36	175.45	2.85	162.61	4.12
y_2	350.95	13.59	342.17	10.85	346.25	9.19	383.78	8.33	344.84	10.50
κ	-0.15	0.33	0.17	0.04	0.00	0.00	0.00	0.00	0.07	0.04
γ	3.14	3.24	0.00	0.00	1.69	0.40	0.00	0.00	1.00	0.00
RSS	29,792		30,103		29,860		35,940		29,938	
$\hat{\sigma}$	17.90		17.90		17.82		19.45		17.85	
n	97		97		97		97		97	
df	93		94		94		95		94	

F-tests			F	P	F	P	F	P	F	P
vs Case 1			0.969	0.328	0.211	0.647	9.596	0.000	0.455	0.502
vs Case 2							18.229	0.000		
vs Case 3							19.142	0.000		
vs Case 5							18.846	0.000		

	Multiplicative									
	Case 1		Case 2		Case 3		Case 4		Case 5	
Parameter	Est.	se	Est.	se	Est.	se	Est.	se	Est.	se
y_1	160.60	3.18	161.89	2.93	160.97	3.06	171.02	2.45	161.39	2.97
y_2	349.16	17.87	336.05	12.38	342.92	10.42	397.59	10.35	340.16	12.19
κ	-0.15	0.35	0.19	0.04	0.00	0.39	0.00	0.00	0.08	0.04
γ	3.16	3.32	0.00	0.00	1.80	0.00	0.00	0.00	1.00	0.00
RSS	0.517		0.523		0.518		0.645		0.520	
$\hat{\sigma}$	0.0746		0.0746		0.0743		0.0824		0.0744	
n	97		97		97		97		97	
df	93		94		94		95		94	

F-tests			F	P	F	P	F	P	F	P
vs Case 1			1.008	0.318	0.183	0.669	11.491	0.000	0.466	0.497
vs Case 2							21.972	0.000		
vs Case 3							22.999	0.000		
vs Case 5							22.646	0.000		

Note: Shaded boxes denote parameters set at a specified number (e.g., 0.0 or 1.0).

Table A.5. Schnute growth models parameter estimates, standard error, RSS, and F-tests for fits of cutthroat trout (sexes pooled) at Florence Lake.

Additive										
	Case 1		Case 2		Case 3		Case 4		Case 5	
Parameter	Est.	se	Est.	se	Est.	se	Est.	se	Est.	se
y_1	160.24	3.86	162.79	2.97	161.06	3.34	176.13	1.97	161.71	3.10
y_2	344.29	7.19	340.13	6.14	342.29	5.47	369.64	4.82	341.62	5.96
κ	-0.09	0.22	0.14	0.03	0.00	0.00	0.00	0.00	0.05	0.02
γ	2.54	2.34	0.00	0.00	1.55	0.26	0.00	0.00	1.00	0.00
RSS	75,534		75,892		75,592		88,134		75,671	
$\hat{\sigma}$	18.04		18.05		18.01		19.41		18.02	
n	236		236		236		236		236	
df	232		233		233		234		233	

F-tests			F	P	F	P	F	P	F	P
vs Case 1			1.100	0.295	0.179	0.673	19.350	0.000	0.420	0.517
vs Case 2							37.584	0.000		
vs Case 3							38.658	0.000		
vs Case 5							38.375	0.000		

Multiplicative										
	Case 1		Case 2		Case 3		Case 4		Case 5	
Parameter	Est.	se	Est.	se	Est.	se	Est.	se	Est.	se
y_1	159.22	2.54	161.10	2.23	159.90	2.39	171.26	1.75	160.41	2.28
y_2	344.58	9.58	335.35	7.44	339.24	6.40	381.61	5.95	337.98	7.24
κ	-0.16	0.23	0.16	0.03	0.00	0.26	0.00	0.00	0.06	0.03
γ	3.28	2.27	0.00	0.00	1.65	0.00	0.00	0.00	1.00	0.00
RSS	1.309		1.322		1.312		1.561		1.315	
$\hat{\sigma}$	0.0751		0.0753		0.0750		0.0817		0.0751	
n	236		236		236		236		236	
df	232		233		233		234		233	

F-tests			F	P	F	P	F	P	F	P
vs Case 1			2.239	0.136	0.554	0.458	22.348	0.000	1.083	0.299
vs Case 2							42.232	0.000		
vs Case 3							44.226	0.000		
vs Case 5							43.596	0.000		

Note: Shaded boxes denote parameters set at a specified number (e.g., 0.0 or 1.0).

Table A.6. F, univariate, and multivariate tests supporting comparison of growth (Schnute growth model case 3) between male and female cutthroat trout at Florence Lake.

	Female		Male		Pooled	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
y_1	157.35	3.72	160.97	3.06	159.90	2.39
y_2	338.44	7.92	342.92	10.42	339.24	6.40
γ	1.58	0.33	1.80	0.39	1.65	0.26
RSS	0.7483		0.5184		1.3124	
df	136		94		233	

F-test

RSS_y	1.3124	F	2.7652	Conclusion
RSS_x	1.2667	F_{crit}	2.6439	
df_y	233	P-value	0.0427	Reject H_0
df_x	230			

Univariate Tests

Parameter	*z*	*f*	P-value	Conclusion
y_1	0.7526	229.9793	0.4525	Fail to reject H_0
y_2	0.3423	190.0636	0.7325	Fail to reject H_0
γ	0.4279	203.2872	0.6692	Fail to reject H_0

Table A.7. Hotelling T^2 calculations for the test of equality between sexes for cutthroat trout, Florence Lake.

Parameters	Female				Male		
y_1	157.35				160.97		
y_2	338.44				342.92		
γ	1.58				1.80		
Correlations	1.00	0.30	-0.62		1.00	0.26	-0.51
	0.30	1.00	-0.87		0.26	1.00	-0.89
	-0.62	-0.87	1.00		-0.51	-0.89	1.00
S_i	13.82	8.95	-0.76		9.37	8.19	-0.61
	8.95	62.67	-2.27		8.19	108.58	-3.64
	-0.76	-2.27	0.11		-0.61	-3.64	0.15
Σ_i	1921.31	1244.19	-105.54		908.94	794.89	-59.21
	1244.19	8711.77	-314.92		794.89	10532.73	-352.91
	-105.54	-314.92	15.07		-59.21	-352.91	14.94
Σ	1507.56	1060.56	-86.60				
	1060.56	9455.99	-330.44				
	-86.60	-330.44	15.02				
$\Delta\Theta$	-3.625	$\Delta\Theta'$	-3.625	-4.480	-0.219		
	-4.480						
	-0.219						
V	26.39	18.56	-1.52		23.19	17.15	-1.37
	18.56	165.51	-5.78		17.15	171.26	-5.90
	-1.52	-5.78	0.26		-1.37	-5.90	0.26
V^{-1}	0.08	0.03	1.19		0.09	0.03	1.18
	0.03	0.04	1.04		0.03	0.04	1.00
	1.19	1.04	33.49		1.18	1.00	32.51

T_1^2	8.471	T_3^2	8.354
P-value	0.041	P-value	0.044
f	230	f_e	198.7
num. f	3 =p	num. f	3
den. f	228 =f-p+1	den. f	196.7
F_{crit}	2.644	F_{crit}	2.651
T^{*2}	8.002	T^{*2}	8.033
Conclusion:	Reject	Conclusion:	Reject

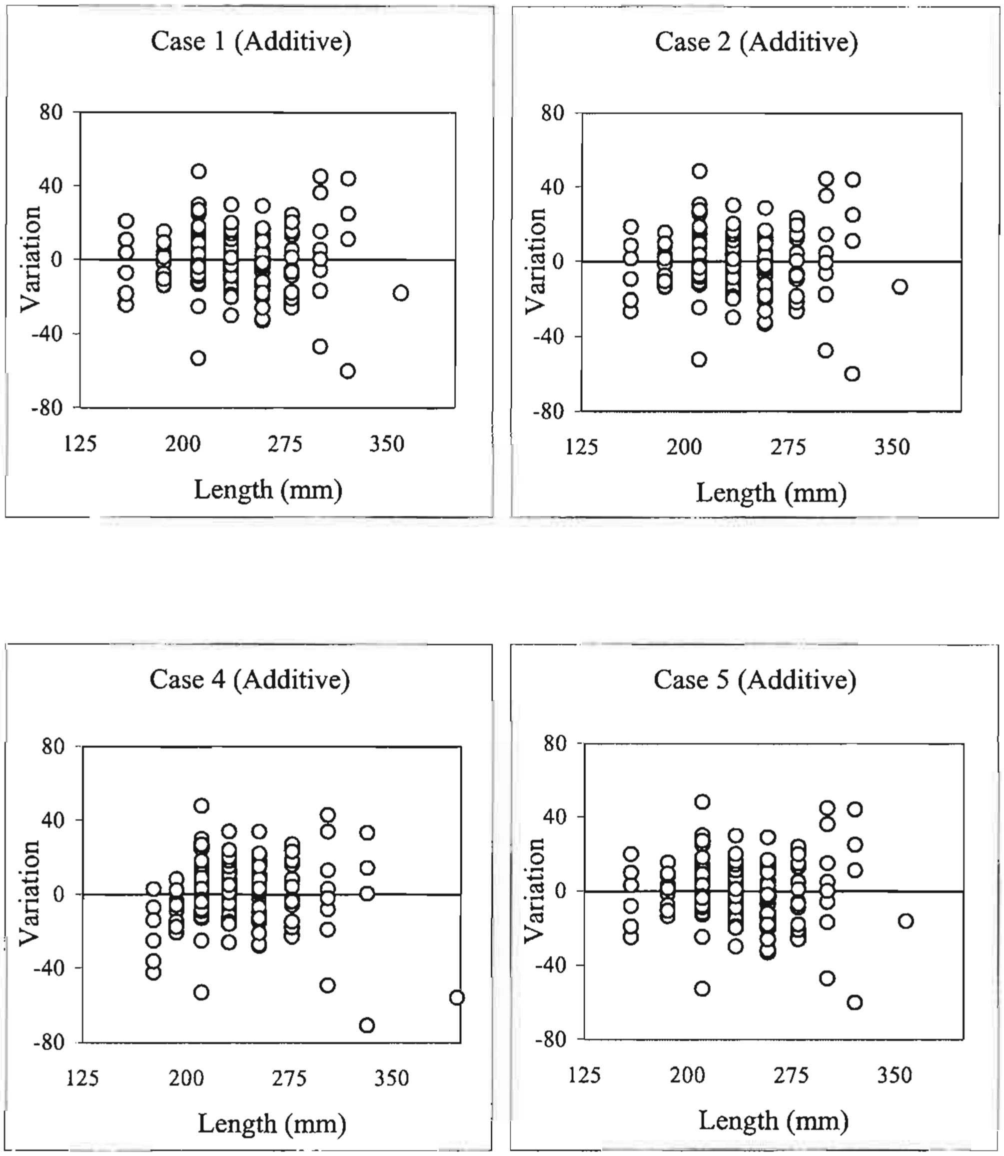


Figure A.1. Residuals plots for Schnute growth model cases 1, 2, 4, and 5 (additive error) for female cutthroat trout at Florence Lake.

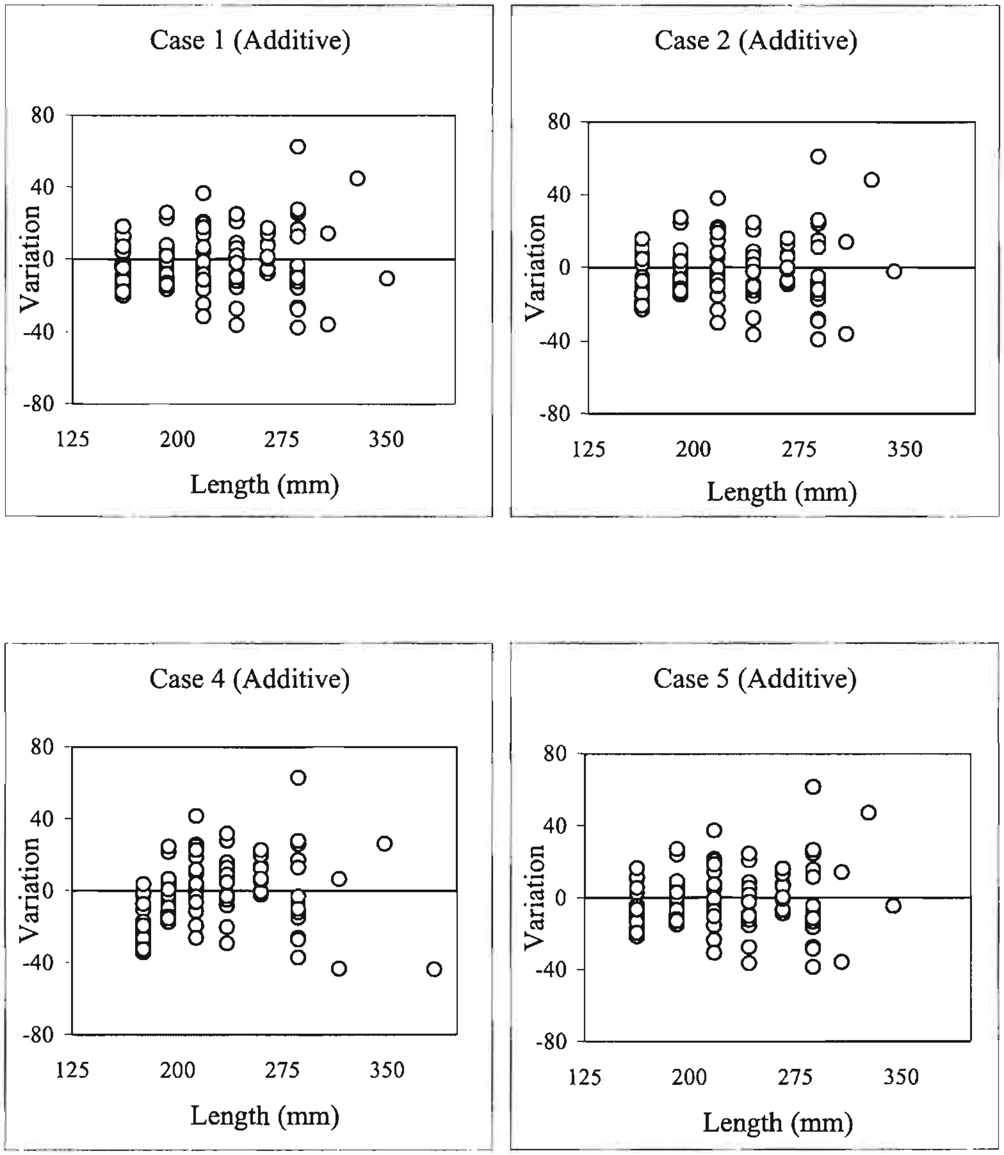


Figure A.2. Residuals plots for Schnute growth model cases 1, 2, 4, and 5 (additive error) for male cutthroat trout at Florence Lake.

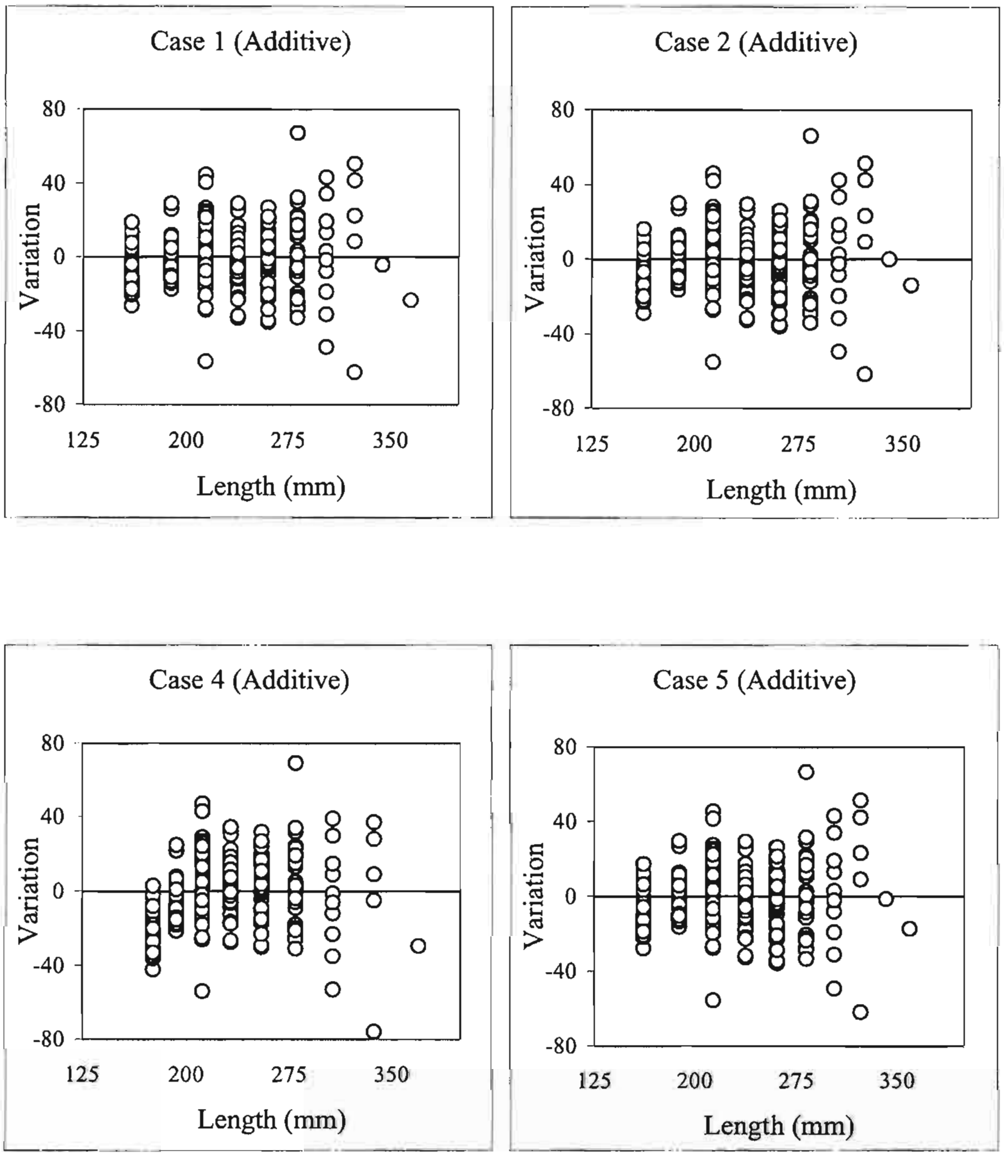


Figure A.3. Residuals plots for Schnute growth model cases 1, 2, 4, and 5 (additive error) for cutthroat trout (sexes pooled) at Florence Lake.

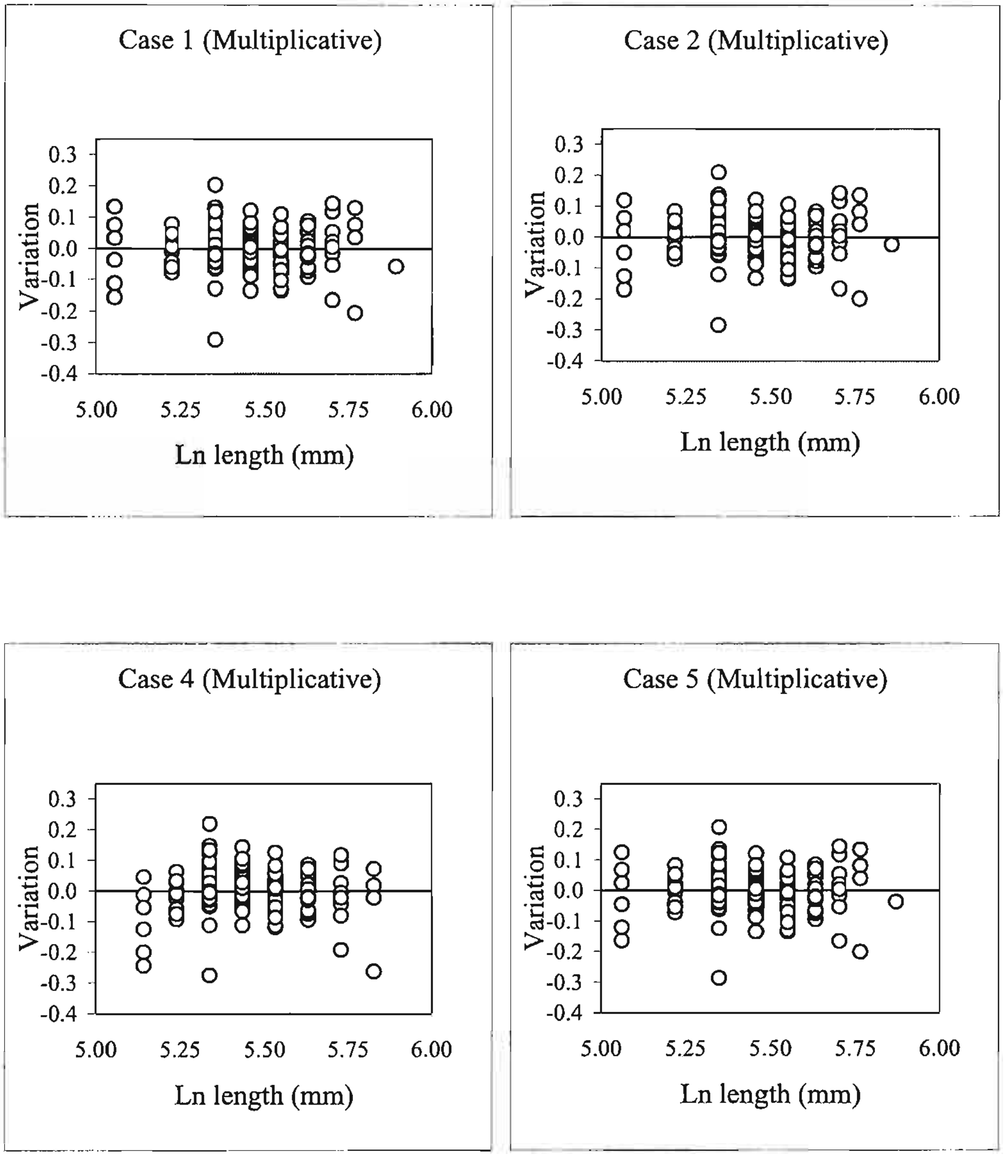


Figure A.4. Residuals plots for Schnute growth model cases 1, 2, 4, and 5 (multiplicative error) for female cutthroat trout at Florence Lake.

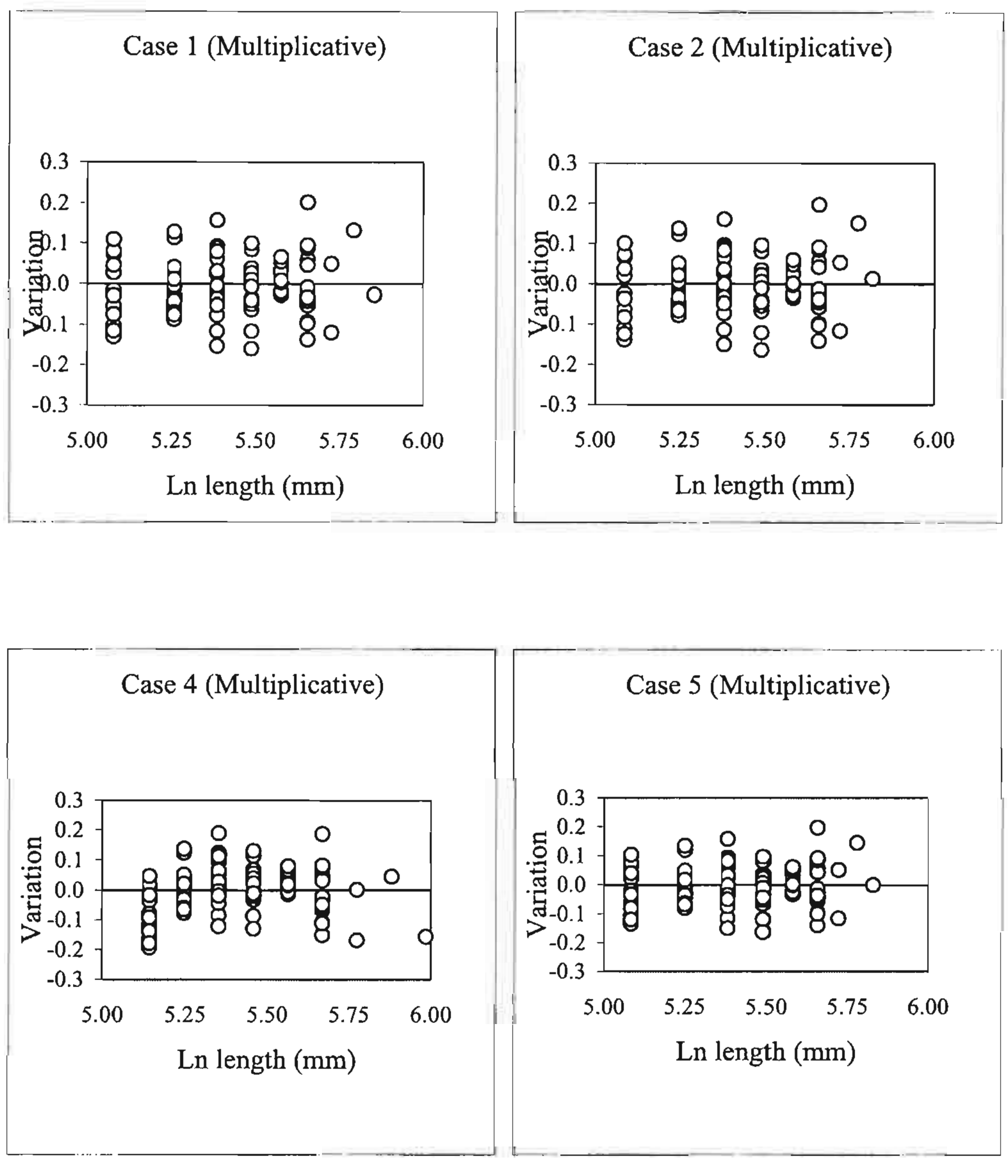


Figure A.5. Residuals plots for Schnute growth model cases 1, 2, 4, and (multiplicative error) for male cutthroat trout at Florence Lake.

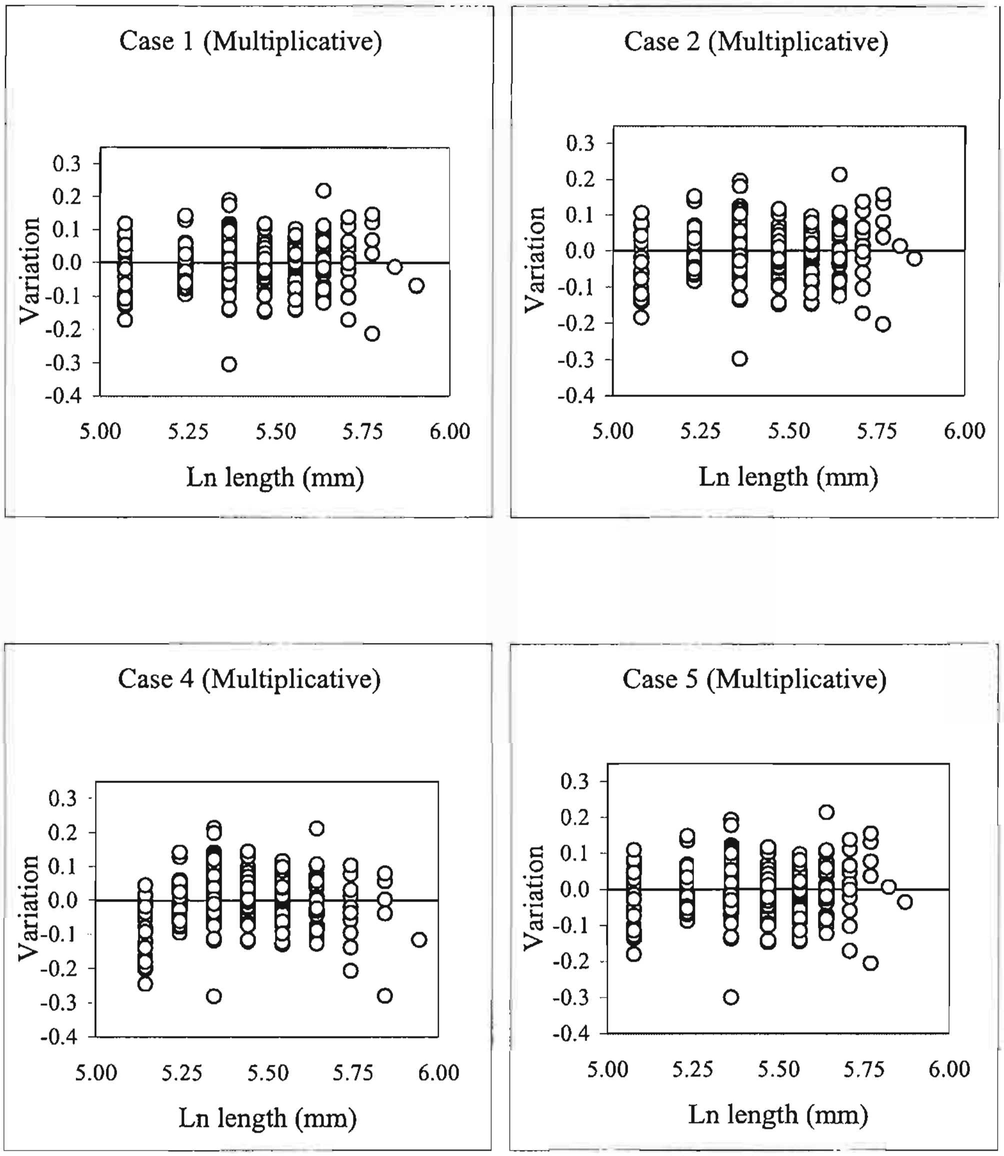


Figure A.6. Residuals plots for Schnute growth model cases 1, 2, 4, and 5 (multiplicative error) for cutthroat trout (sexes pooled) at Florence Lake.

Appendix B.1. Per-recruit analysis population statistics output for pristine population.

Age	Population Abundance	Female Spawning Population	Biomass (kg)	Female Spawning Biomass	Gonad Volume	Catch	Yield (kg)	Egg Production
Length-based								
3	4,000	18	153.9	0.9	21,331	0	0.00	1,890
4	2,426	121	153.6	11.2	310,076	0	0.00	20,163
5	1,472	250	139.9	31.3	968,888	0	0.00	53,112
6	893	263	119.2	41.7	1,410,657	0	0.00	67,358
7	541	204	96.7	40.3	1,480,802	0	0.00	62,142
8	328	139	75.4	33.6	1,338,628	0	0.00	49,709
9	199	89	57.0	26.1	1,118,147	0	0.00	37,082
10	121	55	41.8	19.4	886,080	0	0.00	26,571
11	73	34	29.9	13.9	671,458	0	0.00	18,491
12	44	21	20.7	9.7	487,722	0	0.00	12,544
13	27	13	14.0	6.5	340,618	0	0.00	8,314
14	16	8	9.2	4.3	229,876	0	0.00	5,398
Total	10,141	1,213	911.3	239.0	9,264,284	0	0.00	362,773
Age-based								
3	4,000	10	155.7	0.4	7,725	0	0.00	831
4	2,426	56	152.0	3.5	82,554	0	0.00	6,810
5	1,472	210	136.6	19.5	530,921	0	0.00	35,179
6	893	320	115.4	41.4	1,272,570	0	0.00	70,089
7	541	242	93.0	41.6	1,415,692	0	0.00	66,535
8	328	152	72.2	33.5	1,246,312	0	0.00	51,030
9	199	93	54.4	25.4	1,021,762	0	0.00	37,063
10	121	56	40.0	18.7	805,964	0	0.00	26,260
11	73	34	28.8	13.5	617,549	0	0.00	18,283
12	44	21	20.4	9.5	461,932	0	0.00	12,549
13	27	13	14.2	6.6	338,510	0	0.00	8,510
14	16	8	9.8	4.6	243,701	0	0.00	5,711
Total	10,141	1,214	892.7	218.1	8,045,190	0	0.00	338,850

Appendix B.2. Per-recruit analysis population statistics output for 9-inch (229 mm) MSL at $F_{N50\%}$ BRP.

Age	Population Abundance	Female Spawning Population	Biomass (kg)	Female Spawning Biomass	Gonad Volume	Catch	Yield (kg)	Egg Production
Length-based		F=0.436						
3	4,000	18	153.9	0.9	21,331	92	4.79	1,890
4	2,356	113	147.9	10.4	286,906	281	22.15	18,752
5	1,214	186	110.4	22.7	695,715	245	25.40	38,706
6	550	145	68.0	22.1	734,492	134	17.85	35,900
7	232	80	37.6	14.9	536,732	61	10.33	23,230
8	94	37	19.5	8.5	328,920	26	5.46	12,665
9	38	16	9.7	4.4	183,328	10	2.74	6,321
10	15	7	4.7	2.2	96,146	4	1.33	2,998
11	6	3	2.2	1.0	48,053	2	0.62	1,373
12	2	1	1.0	0.5	22,994	1	0.28	611
13	1	0	0.4	0.2	10,571	0	0.13	265
14	0	0	0.2	0.1	4,691	0	0.05	113
Total	8,509	607	555.5	87.8	2,969,878	857	91.14	142,825
Age-based		F=0.388						
3	4,000	10	155.7	0.4	7,725	46	1.80	831
4	2,391	55	149.8	3.4	81,345	259	16.24	6,710
5	1,251	178	116.2	16.6	451,504	292	27.09	29,917
6	537	193	69.5	24.9	766,015	137	17.71	42,190
7	222	99	38.1	17.0	580,462	57	9.80	27,281
8	91	42	20.1	9.3	346,799	23	5.17	14,200
9	38	18	10.3	4.8	192,881	10	2.64	6,996
10	15	7	5.1	2.4	103,211	4	1.32	3,363
11	6	3	2.5	1.2	53,648	2	0.64	1,588
12	3	1	1.2	0.6	27,222	1	0.31	740
13	1	1	0.6	0.3	13,533	0	0.15	340
14	0	0	0.3	0.1	6,609	0	0.07	155
Total	8,556	607	569.3	81.0	2,630,953	831	82.94	134,311

Appendix B.3. Per-recruit analysis population statistics output for 11-inch (279 mm) MSL at $F_{E40\%}$ BRP.

Age	Population Abundance	Female Spawning Population	Biomass (kg)	Female Spawning Biomass	Gonad Volume	Catch	Yield (kg)	Egg Production
Length-based		F=1.985						
3	4,000	18	153.9	0.9	21,331	4	0.22	1,890
4	2,423	121	153.3	11.2	308,724	69	7.23	20,084
5	1,417	232	132.0	28.4	869,599	225	30.36	48,303
6	692	180	82.8	26.0	846,312	215	33.24	42,844
7	262	82	36.3	13.1	444,141	106	17.98	21,155
8	81	28	12.3	4.7	164,839	37	6.69	7,516
9	22	8	3.6	1.4	50,269	11	2.03	2,221
10	6	2	0.9	0.4	13,716	3	0.55	592
11	1	1	0.2	0.1	3,523	1	0.14	150
12	0	0	0.1	0.0	879	0	0.03	37
13	0	0	0.0	0.0	218	0	0.01	9
14	0	0	0.0	0.0	54	0	0.00	2
Total	8,906	671	575.4	86.3	2,723,606	670	98.50	144,803
Age-based		F=2.160						
3	4,000	10	155.7	0.4	7,725	2	0.07	831
4	2,425	56	152.0	3.5	82,510	16	0.98	6,807
5	1,459	208	135.4	19.3	526,313	114	10.57	34,874
6	797	286	103.1	37.0	1,136,942	355	45.96	62,620
7	218	98	37.5	16.8	571,192	155	26.70	26,845
8	21	10	4.6	2.1	79,479	16	3.46	3,254
9	2	1	0.4	0.2	7,830	1	0.31	284
10	0	0	0.0	0.0	716	0	0.03	23
11	0	0	0.0	0.0	63	0	0.00	2
12	0	0	0.0	0.0	5	0	0.00	0
13	0	0	0.0	0.0	0	0	0.00	0
14	0	0	0.0	0.0	0	0	0.00	0
Total	8,922	668	588.8	79.3	2,412,776	659	88.06	135,540

Appendix B.4. Per-recruit analysis population statistics output for 11-inch (279 mm) MSL at $F_{GV45\%}$ BRP.

Age	Population Abundance	Female Spawning Population	Biomass (kg)	Female Spawning Biomass	Gonad Volume	Catch	Yield (kg)	Egg Production
Length-based		F=0.697						
3	4,000	18	153.9	0.9	21,331	1	0.08	1,890
4	2,425	121	153.5	11.2	309,598	27	2.87	20,135
5	1,450	243	136.7	30.1	928,420	107	15.06	51,170
6	798	224	101.5	34.0	1,130,053	134	22.51	55,366
7	383	134	60.8	24.0	852,321	93	18.04	37,805
8	162	63	30.9	13.1	494,574	47	10.49	20,010
9	62	26	14.0	6.2	246,338	20	5.10	9,132
10	23	10	5.9	2.6	111,377	8	2.22	3,801
11	8	3	2.3	1.1	47,031	3	0.90	1,488
12	3	1	0.9	0.4	18,824	1	0.35	557
13	1	0	0.3	0.2	7,204	0	0.13	201
14	0	0	0.1	0.1	2,654	0	0.05	71
Total	9,315	843	660.9	123.9	4,169,723	443	77.80	201,627
Age-based		F=0.765						
3	4,000	10	155.7	0.4	7,725	1	0.02	831
4	2,426	56	152.0	3.5	82,538	6	0.35	6,809
5	1,467	209	136.2	19.4	529,285	42	3.88	35,071
6	858	308	110.9	39.8	1,222,800	167	21.65	67,348
7	393	175	67.5	30.2	1,026,656	152	26.15	48,251
8	124	57	27.3	12.6	470,390	53	11.67	19,260
9	36	17	9.7	4.5	182,145	15	4.20	6,607
10	10	5	3.3	1.6	67,011	4	1.44	2,183
11	3	1	1.1	0.5	23,909	1	0.48	708
12	1	0	0.4	0.2	8,326	0	0.16	226
13	0	0	0.1	0.1	2,840	0	0.05	71
14	0	0	0.0	0.0	952	0	0.02	22
Total	9,316	838	664.2	112.7	3,624,577	442	70.08	187,388

Appendix B.5 Per-recruit analysis population statistics output for 12-inch (305 mm) MSL at $F_{GV45\%}$ BRP.

Age	Population Abundance	Female Spawning Population	Biomass (kg)	Female Spawning Biomass	Gonad Volume	Catch	Yield (kg)	Egg Production
Length-based		F=1.788						
3	4,000	18	153.9	0.9	21,331	0	0.02	1,890
4	2,426	121	153.6	11.2	309,978	8	0.90	20,157
5	1,465	248	138.9	31.0	955,557	62	10.14	52,496
6	842	241	108.5	36.9	1,229,241	127	24.26	60,019
7	416	147	65.5	25.9	909,328	110	23.17	40,971
8	171	66	30.4	12.8	465,012	59	13.22	19,826
9	60	24	11.6	5.0	187,584	24	5.60	7,688
10	19	8	3.9	1.7	65,149	8	1.99	2,595
11	6	2	1.2	0.5	20,611	3	0.64	805
12	2	1	0.4	0.2	6,163	1	0.19	237
13	0	0	0.1	0.0	1,784	0	0.06	68
14	0	0	0.0	0.0	509	0	0.02	19
Total	9,407	877	668.0	126.2	4,172,246	402	80.19	206,770
Age-based		F=2.743						
3	4,000	10	155.7	0.4	7,725	0	0.01	831
4	2,426	56	152.0	3.5	82,549	2	0.10	6,810
5	1,470	209	136.5	19.4	530,456	13	1.16	35,148
6	882	316	114.1	40.9	1,257,676	79	10.24	69,269
7	474	212	81.5	36.4	1,240,345	224	38.50	58,294
8	121	56	26.6	12.3	459,040	92	20.24	18,795
9	8	4	2.2	1.0	41,555	7	1.78	1,507
10	0	0	0.1	0.1	2,293	0	0.09	75
11	0	0	0.0	0.0	115	0	0.00	3
12	0	0	0.0	0.0	6	0	0.00	0
13	0	0	0.0	0.0	0	0	0.00	0
14	0	0	0.0	0.0	0	0	0.00	0
Total	9,382	863	668.7	114.1	3,621,760	416	72.13	190,734