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Abstract

Ratliff et al. (1996) found rapid growth occurring when juvenile adfluvial bull trout of Lake Billy w0ly

Cases 2, 3, and 4, are sub-models of Schnute's generalized model (case 1). Given the ubiquity of the VB in fish stock assessments, the VB subcase model was also evaluated, making five models in all that were assessed.

All parameter estimates were found by the minimization of the sum of squares (SS) based on an additive error assumption and using a Gauss-Newton algorithm. Estimates were calculated through an iterative approach using SAS version 9.1 (SAS Inc. Cary, North Carolina). Models were compared using the Akaike information criterion (AIC). The model with the lowest AIC was selected; however all models with $\Delta AIC < 2$ were assumed to have equal support for use with the data (Burnham and Anderson 2002).

JOM Group Growth Comparisons

To explore the dynamics of growth in migratory bull trout, the Schnute VB subcase was also fitted to the age estimates derived from pelvic fin rays for individual JOM groups. An analysis of the residual sum of squares (ARSS) proposed by Chen et al. (1992) was utilized to test for significant differences between the growth curves of the different groups with the null hypothesis that all curves are coincident, or each group is a sample from the same population. If the curves were not found to be coincident (a rejection of the null hypothesis;

$\alpha = 0.05$), then bootstrap confidence intervals (CI's) were calculated and examined to determine differences between specific groups. Bootstrapping was conducted by randomly resampling from the population (15 000 times) with replacement. Confidence intervals were calculated using a first order bias correction on the percentile method by adjusting on the basis of the proportion of bootstrap estimates less than the original estimates (Haddon 2001). The groups being compared were determined to be significantly different if bootstrap confidence intervals did not overlap on any one parameter. Bootstrap parameter clouds were also compared.

Age at Sexual Maturation

Ages were assigned and integrated with the maturation data determined by Hanson et al. (2006). We assumed the youngest mature fish was the youngest age of maturation. JOM age assignments by gender were also integrated with the maturity data to gain insight into growth, maturity, and outmigration relationships.

Results

Multiple cases of Schnute models fitted to the

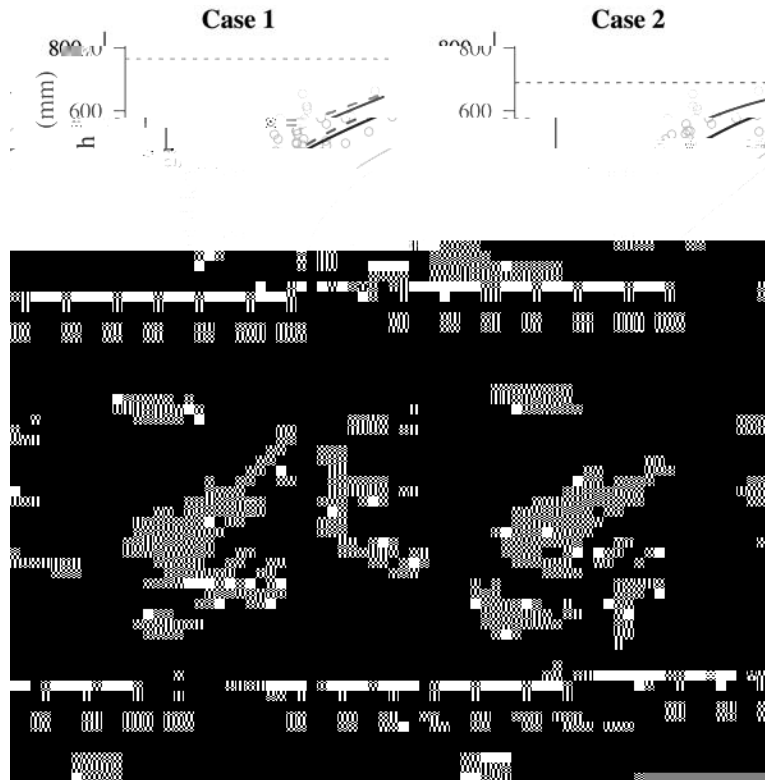


Figure 2. Schnute model cases (curves) fitted to age-length data for NFCR migratory bull trout. The age-length model is derived from age estimates from 120 pelvic fin rays collected during the spring of 2005. Points represent final age determinations. Horizontal dashed lines represent asymptotic length for the VB sub-case and for Case 2.

TABLE 2. AIC values for four age-length growth models (Schnute 1981) and the VB subcase for NFCR migratory bull trout. Ages were assigned from pelvic fin rays collected in the spring of 2005.

Model Case	Df	Parameters	AIC	ΔAIC	Deviance
Case 3	4	3	1265.42	0.00	249 733.8
VB subcase	4	3	1265.74	0.32	250 391.7
Case 2	4	3	1266.13	0.70	251 203.3
Case 1	5	4	1267.39	1.97	249 668.6
Case 4	3	2	1278.79	13.37	283 854.0

Table 2), the VB sub-case, case 2, and the fully parameterized case 1, had AIC values of only 0.32, 0.70, and 1.97 lower. The case 4 model had the highest AIC (1278.8). Case 1, with $a = -0.06$, depicted unbounded growth while the VB sub-case and Case 2 were both asymptotic. Asymptotic lengths for these models were 766 mm for the VB sub-case and 690 mm for Case 2.

In comparisons of JOM growth rates, spacing between annuli increased by 50% or more following the first to third annuli for 98% (118/120) of the bull trout fin rays examined. Only two samples showed consistent annuli spacing throughout the cross-sections (no increases of 50% were found) and were therefore not assigned a JOM age. The percentages of the assigned ages were 14%

(17/120) for JOM 1, 57% (68/120) for JOM 2, and 28% (33/120) for JOM 3 (Table 3).

A significant relationship was found between assigned JOM ages and overall growth rates. The null hypothesis for the VB subcase that the growth curves derived from age-length data for JOM groups were similar was rejected ($F = 12.45$, $df = 115$, $P < 0.001$), indicating that at least one growth curve among JOM 1, JOM 2, and JOM 3 was significantly different. All parameters successfully converged on estimates during the nonlinear iterations for growth curves for all three JOM groups (Table 4).

Further analysis of bootstrap CI overlap indicated differences in parameter estimates between JOM 1 and JOM 3. The Schnute VB subcase converged on parameter estimates for 14 849/15 000 bootstrap iterations and found non-overlapping CI's for the estimates for 14 849 of the nonlinear

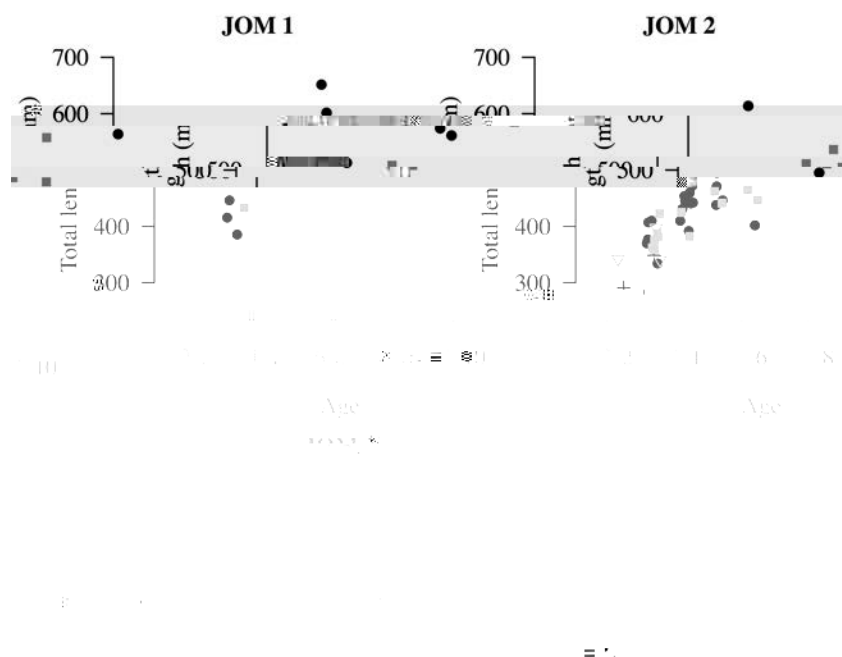


Figure 4. Total lengths at ages for NFCR migratory bull trout. Ages were estimated from pelvic fin rays. All were fish were assigned an age of juvenile outmigration (JOM 1, JOM 2, and JOM 3).

age 4, of which two were males (one assigned to JOM 2 at 345 mm TL and one to JOM 3 at 325 mm TL) and two were females (both assigned to JOM 2 at 340 and 397 mm TL). There were no immature fish assigned to the JOM 1 group. The remaining 73 mature adults had TLs ranging from 334 to 654 mm (mean = 452 mm, SD = 71.1 mm). There were no mature age-4 fish that were classified into the JOM 3 group and there were no age 3 fish documented as mature. There was one mature female (425 mm TL) that was not assigned to a JOM group and was aged as 9.

Discussion

Of the five models evaluated for characterizing growth of migratory bull trout from ages 3 to 11 in the NFCR, four of them performed comparably; only Case 4, which assumes growth is a power

function with age as the exponent (Quinn II and Deriso 1999), clearly performed less effectively. Although Case 4 can be useful for modeling portions of a fish's lifespan, it may be better suited for larval or juvenile stages because it depicts unbounded accelerated growth (Schnute 1981). This case does not seem biologically plausible for modeling bull trout growth from ages 3 to 11 because decreasing growth with age is a typical pattern for salmonids and has recently been reported for migratory bull trout (Al-Chokhachy et al. 2015). All of the remaining models incorporated this pattern and all adequately described growth for the age range studied.

Cases 1 and 3 both depicted unbounded decelerated growth while the VB sub-case and Case 2 were both asymptotic models; models that are bound by a hypothetical maximum size. With

documented (ages 5 to 7, Flathead Lake system, Fraley and Shepard 1989; Goetz 1989). Mogen and Kaeding (2005) reported that migratory bull trout from the St. Mary's River Drainage, Montana reached maturity and migrated upstream to spawn at age 5 at about 300 mm TL. Pratt (1985) found first year spawning occurring at ages 4 to 6 in the adfluvial population of Lake Pend Oreille, only 4 % of the age-4 class was mature. Frequent age-4 maturation of bull trout in the NFCR drainage is supported by the peaks in redd counts every four years since 1999 (Erhardt and Scarnecchia 2014). Although it is not specifically known why the NFCR bull trout population is maturing at younger ages than these other drainages, it may be related to the higher growth rates or longer growing seasons in the NFCR, including Dworshak Reservoir, than

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