

## STATUS AND DYNAMICS OF A BURBOT POPULATION ON THE EDGE

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**Abstract:** We examined the status and population characteristics of Kootenai River burbot *Lota lota* using capture-recapture data from 1993-2004. Our objective was to determine the time remaining before this population becomes functionally extinct and to help guide conservation efforts. A total of 403 burbot were captured from 1993 through 2004 (primarily with baited hoop nets), of which 300 were tagged and released, 31 were not tagged, and 72 were recaptures of fish tag up to four years prior. Hoop net catch per unit of effort (CPUE) decline precipitously from 0.054 CPUE in 1996 to 0.008 CPUE in 2004. Mean burbot length increased about 8mm/yr from 516 mm in 1993 to 629 mm in 2004. Two models were developed for capture-recapture analysis, one which included effort data through a series river reaches and one without effort data. The effort model appeared to be more reliable and suggested an average annual mortality of 63%, an average annual recruitment of 77 fish, and an average estimate of 148 burbot in the Kootenai River from 1996 through 2004. Average declines in recruitment and population abundance were estimated to be 21% and 14% per year, respectively, resulting in estimates of only 20 recruits and a population size of only 50 burbot in 2004. These data confirm that Kootenai River burbot are in serious decline and may already have passed the point of functional extinction where the population could be expected to recover if favorable habitat conditions were restored.

## ***Introduction***

The Kootenai River is at the northern edge of the continental United States but near the southern edge of the circumpolar distribution of the burbot (*Lota lota*) (McPhail and Lindsey 1970). Although burbot are globally widespread and abundant throughout much of their historical range (Muth and Smith 1974; Bruesewitz 1990; Evensen and Hansen 1991; Edsall et al. 1993; Maitland and Lyle 1996; Arndt and Hutchinson 2000), the Kootenai population appears to be in serious decline (Paragamian *et al.* 2000). Popular burbot fisheries in Kootenay Lake and the Kootenai River had collapsed by the 1970s (Paragamian *et al.* 2000). Neither population has recovered despite closure of the fisheries (Paragamian *et al.* 2000). Extensive alteration of the Kootenai ecosystem may have shifted habitat conditions past the margin of suitability for burbot. It is unclear whether significant numbers are still present and whether recovery is feasible.

Lake, river, and tributary spawning life histories were historically represented among Kootenai burbot but all population elements appear to have failed. Small numbers remain in the Duncan River at the north end of Kootenay Lake but burbot are now rarely observed in the South or West arms of Kootenay Lake or the Kootenai River between the lake and Kootenai Falls. Burbot remain common in the upper Kootenai system upstream from Kootenai Falls including Libby Reservoir and the upper river. Kootenai burbot were petitioned for listing as threatened under the U.S. Endangered Species but the U.S. Fish and Wildlife Service found in 2003 that listing was not warranted because this population does not represent a distinct population segment. Burbot in the lower Kootenai River and Kootenay Lake of Idaho and British Columbia are genetically different from burbot stocks in Montana upstream of Kootenai Falls (Paragamian *et al.* 1999) but the difference not deemed sufficient to warrant formal protection.

Burbot represent a significant historical and cultural resource to the local region and are subject of a regional Burbot Conservation Strategy developed by local stakeholders (KVRI Burbot Committee 2005). Burbot have been subject to extensive sampling efforts in the Kootenai River over the last decade and this information is critical for the development of effective conservation and recovery measures. This paper synthesizes results of this long term sampling program to determine current population trend, abundance, and demographic characteristics.

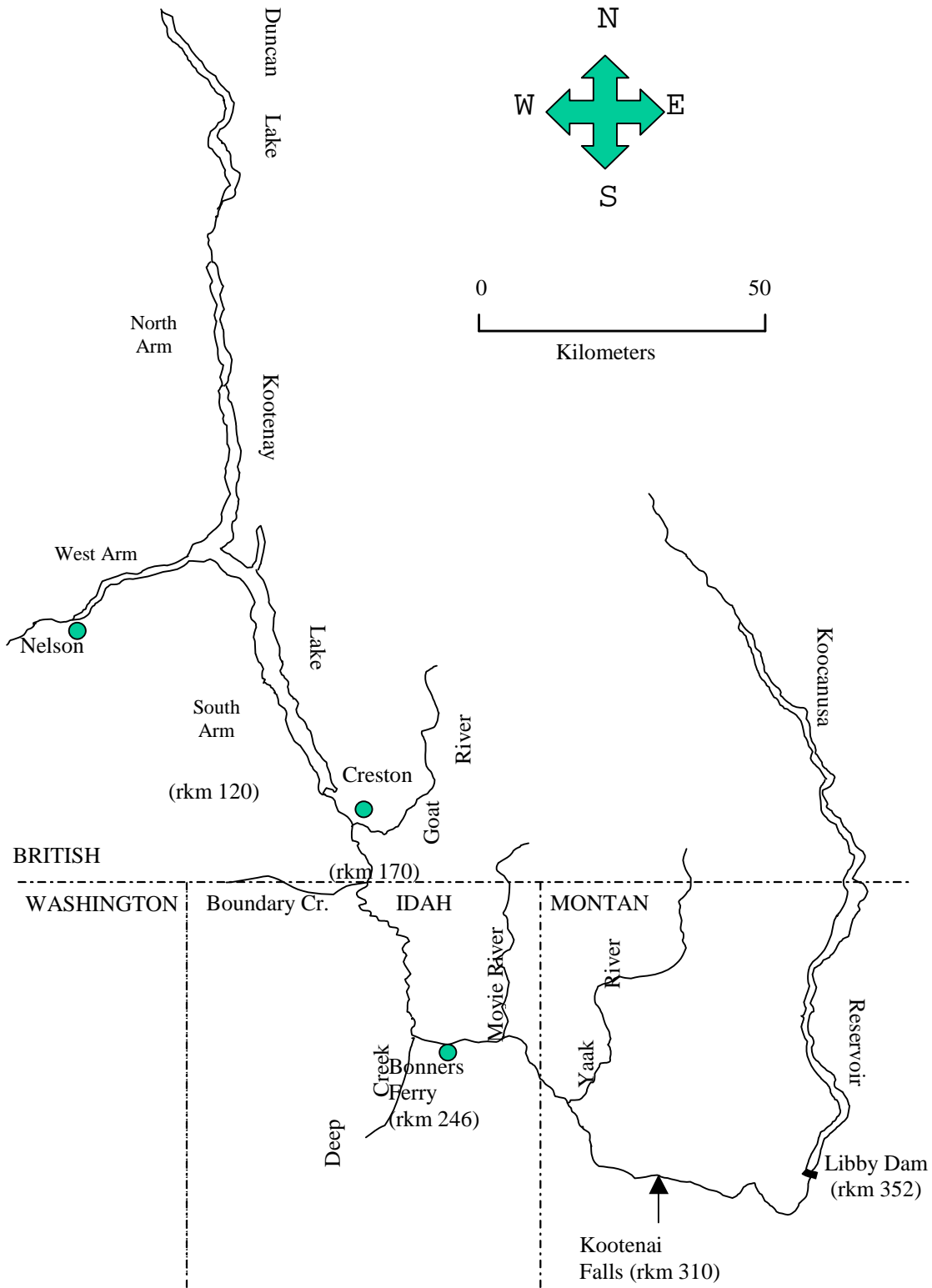


Figure 1. Location of Kootenay Lake, the Kootenai River, Lake Koocanusa, and major tributaries in the basin; river kilometer measurements are from the northernmost arm of Kootenay Lake.

## **Methods**

### **Study Area**

The Kootenai River (spelled Kootenay for Canadian waters) is one of the largest tributaries to the Columbia River. Originating in Kootenay National Park, BC, the river flows south into Montana, where Libby Dam impounds water into Canada and forms Lake Koocanusa (Figure 1). From Libby Dam, the river flows west and then northwest into Idaho, then north into BC and Kootenay Lake. The Kootenai River at Porthill, Idaho (i.e. @ BC border), drains about 35,490 km<sup>2</sup>; the reach in Idaho is 106 km long. Kootenay Lake drains out the West Arm, and eventually the river joins the Columbia River near Castlegar, BC.

The Idaho reach is characterized by three different channel types: steep canyon walls and a high gradient (~0.6 m/km) typify the corridor from the Montana Border to the Moyie River; about 1 km below the Moyie River downstream to Bonners Ferry the river follows a braided channel; downstream of Bonners Ferry the river meanders through a broad floodplain with a lower gradient of about 0.02 m/km. Tributary streams of the Kootenai River are typically high gradient as they pass through mountain canyons but revert to lower gradients when they reach the valley floor.

### **Adult Sampling**

The Kootenai River Fisheries Investigation was initiated in 1993 by the Idaho Department of Fish and Game (IDFG) to document burbot abundance, distribution, size structure, reproductive success, and movement, and to identify factors limiting burbot in the Kootenai River. Sampling continued annually through the spring of 2004. Adult burbot were sampled using baited hoop nets primarily during the winter season to coincide with seasonal migrations. Hoop nets had a maximum diameter of 0.61 m (see Paragamian 1995 for a description of the nets and the method of deployment). Although sampling dates varied annually, sampling seasons generally began in the fall and continued through the following spring (Table 1). Catch per unit of effort (CPUE) was measured by a 24 h set period for each net, with one net day equaling one unit of effort.

Nets were deployed in deep areas (usually the thalweg) of the Kootenai River between rkm 123 (South Arm of Kootenay Lake) and rkm 270 (upstream of the Moyie River), although effort during most years was concentrated around Ambush Rock (rkm 244) near Bonners Ferry, Idaho, Boundary Creek near Porthill, Idaho (rkm 170), and the Goat River, near Creston, BC (rkm 152).

**Table 1. Start and end dates for the winter sampling season, 1993-2004.**

Sampling Season	Start Date	End Date
Wtr 1993	March 1993	May 1993
Wtr 1994	October 1993	April 1994
Wtr 1995	November 1994	February 1995
Wtr 1996	November 1995	March 1996
Wtr 1997	October 1996	March 1997
Wtr 1998	October 1997	May 1998
Wtr 1999	October 1998	April 1999
Wtr 2000	October 1999	April 2000
Wtr 2001	October 2000	March 2001
Wtr 2002	October 2001	April 2002
Wtr 2003	October 2002	March 2003
Wtr 2004	November 2003	March 2004

Nets were usually lifted on Monday, Wednesday, and Friday of each week. Fish captured in hoop nets were identified by species, enumerated, measured for total length (TL), and weighed to the nearest gram (g). Sex of most burbot was determined by a gentle abdominal massage, and the vent was examined for sex products. Some post-spawn fish were also biopsied to determine sex and reproductive status. Most burbot were implanted with a passive integrated transponder (PIT) tag in the left opercular muscle, and a small piece of pelvic fin tissue was collected for genetic analysis and archiving (Paragamian 1999). Burbot not implanted with a PIT tag included those that died during capture or burbot captured during other sampling efforts when the appropriate tagging gear was not present.

In addition to adult burbot sampling efforts by the IDFG, Kootenai River burbot have been targeted by the Montana Department of Fish, Wildlife and Parks (1998 only) as well as the British Columbia Ministry of Water, Land and Air Protection (BCMWLAP; 1996-1999 and 2001-2002; Table 2). Further, Kootenai River burbot have been incidentally caught during summer sturgeon sampling in the Kootenai River.

**Table 2. Summary of adult burbot effort (net days), by location, gear, and year.**

Agency	Target Species	Location	Gear	Season	Year												Total	
					1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004		
IDFG	Burbot	Kootenai River	Hoopnets	Winter	554	910	689	496	1,061	1,241	1,454	1,713	2,085	1,530	1,810	1,965	15,507	
	Sturgeon	Kootenai River	Hoopnets, Set Lines	Summer	?	?	?	?	?	?	?	?	?	?	?	?	?	
BCMELP	Burbot	Kootenay Lake	Hoopnets	Winter	-	-	-	-	541	-	1,056	-	-	-	-	-	1,597	
	Burbot	Kootenay River	Hoopnets	Winter	-	-	-	-	-	-	-	-	-	-	-	172	172	
	Burbot	Kootenay Lake	Set Lines	Winter	-	-	-	-	1,167	-	-	-	-	-	-	-	1,167	
	Burbot	Kootenay Lake	Gill Nets	Winter	-	-	-	-	2	-	-	-	-	-	-	-	2	
	Burbot	Kootenay Lake	Rod-Reel	Winter	-	-	-	-	na	-	-	-	-	-	-	-	0	
	Burbot	Goat River	Fence	Winter	-	-	-	-	-	-	-	-	-	-	26	-	-	26
	Burbot	Kootenay Lake	Cod Traps	Winter	-	-	-	-	-	-	137	-	256	-	-	-	-	393
	Burbot	Kootenay Lake	Remote Operated Vehicle	Winter	-	-	-	-	-	-	-	-	108	-	-	-	-	108
	Burbot	Kootenay Lake	Towable Operated Vehicle	Winter	-	-	-	-	-	-	-	-	-	7	-	-	-	7
	Burbot	Kootenay Lake	Dive Surveys	Winter	-	-	-	-	-	-	5	-	-	-	-	-	-	5
	Burbot	Kootenay Lake	Night Surveys	Winter	-	-	-	-	-	-	na	-	0.52	0.17	-	-	-	0.69
		Sturgeon	Kootenay Lake	Set Lines		?	?	?	?	?	?	?	?	?	?	?	?	?
	MDFG	Burbot	Kootenai River	Hoopnets	Winter	-	-	-	-	-	32	-	-	-	-	-	-	32

Note: Where possible, effort units have been converted to days fished. With the ROV and TOV assessments, effort was measured in number of transects completed. A dash indicates the gear was not used to sample burbot during that particular year. 'NA' indicates that the gear type was used to capture burbot, but effort data were not available for that gear type and year.

### **Larval Sampling**

Larval burbot in the Kootenai River were sampled during spring using paired ½ m nets. Larval nets were towed in a downstream direction using an 8 m boat, with one net at the surface and the other approximately 1.5 m below the surface. The boat motor (150 hp) was operated at 1,000 rpm to maintain uniform towing speed. Current meters were mounted in the mouth of each net, and the volume of water filtered through each net was calculated using total towing time and rotation counts per second from the flow meters multiplied by net mouth area (0.785 m<sup>2</sup>). Tows were made at mid channel in the vicinity of Ambush Rock (rkm 247) because of shallow water and debris near the river margin. Tows downstream to the mouth of the Kootenai River (rkm 124.7) were conducted near the shoreline. In addition, experiments to capture juvenile/age-0 burbot were conducted with minnow traps in 1995 and light traps in 2004.

In addition to these IDFG juvenile sampling efforts, BCMWLAP also conducted night surveys for juvenile burbot in Kootenay Lake, Goat River, and Summit Creek. Annual juvenile sampling effort is summarized in Table 3.

**Table 3. Summary of juvenile burbot sampling effort by location, gear, and year.**

Agency	Target Species	Location	Gear	Season	Year												Total	
					1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004		
IDFG	Burbot	Kootenai River	Mid-water Trawl	Winter	-	-	-	-	-	-	-	-	11,795 m <sup>3</sup>	91,803 m <sup>3</sup>	-	-	-	103,598 m <sup>3</sup>
	Burbot	Kootenai River	D-ring Net	Spring/Summer	-	-	-	na	-	-	-	-	-	-	-	-	-	-
	Burbot	Kootenai River	Drift Net	Spring/Summer	-	-	-	na	-	-	-	-	-	-	-	-	-	-
	Burbot	Kootenai River	Towed Meter Nets	Spring/Summer	-	-	-	na	-	-	-	-	-	-	-	-	-	-
	Burbot	Kootenai River	Shrimp Trawl	Spring/Summer	-	-	51,763 m <sup>3</sup>	na	-	-	-	-	-	-	-	-	-	51,763 m <sup>3</sup>
	Burbot	Kootenai River	Gill Nets	Spring/Summer	-	-	12	-	-	-	-	-	-	-	-	-	-	12
	Burbot	Kootenai River	Hoopnets	Spring/Summer	-	-	244	-	-	-	-	-	-	-	-	-	-	244
	Burbot	Kootenai River	Minnow Traps	Spring/Summer	-	-	94	-	-	-	-	-	-	-	-	-	-	94
	Burbot	Kootenai River	Slat Traps	Spring/Summer	-	-	43	-	-	-	-	-	-	-	-	-	-	43
	Burbot	Kootenai River	Beach Seine	Spring/Summer	-	-	15	-	-	-	-	-	-	-	-	-	-	15
	Burbot	Kootenai River	Electrofishing	Spring/Summer	-	-	0.25	-	-	-	-	-	-	-	-	-	-	0
	Sturgeon	Kootenai River	Hoopnets, Set Lines	Summer	?	?	?	?	?	?	?	?	?	?	?	?	?	?
BCMELP	Burbot	Kootenay Lake	Night Surveys	Winter	-	-	-	-	-	-	na	-	0.52	0.17	?	?	0.69	
	Burbot	Kootenay Lake	Mid-water Trawl	Winter	-	-	-	-	12.2x10 <sup>6</sup> m <sup>3</sup>	-	-	-	-	-	-	-	12.2x10 <sup>6</sup> m <sup>3</sup>	
	Burbot	Kootenay Lake	Electrofishing	Winter	-	-	-	-	-	-	7,044 m <sup>2</sup>	-	-	-	-	-	7,044 m <sup>2</sup>	
	Burbot	Kootenay Lake	Minnow Traps	Winter	-	-	-	-	-	-	61	-	-	-	-	-	61	
	Burbot	Kootenay Lake	Beach Seine	Winter	-	-	-	-	-	-	na	-	-	-	-	-	-	
	Sturgeon	Kootenay Lake	Set Lines		?	?	?	?	?	?	?	?	?	?	?	?	?	

Note: Where possible, effort units have been converted to days fished. For mid-water and shrimp trawl gear, effort was measured in volume of water sampled. IDFG beach seine effort measured by the number of hauls. For electrofishing, IDFG effort was measured in days fished and BC effort in area sampled. A dash indicates the gear was not used to sample burbot during that particular year. 'NA' indicates that the gear type was used to capture burbot, but effort data were not available for that gear type and year.

## Analyses

The capture-recapture data consisted of various categories of fish, defined here as follows: (1) “captures” refers to all fish caught and sampled; (2) “tagged fish” are captures that were successfully tagged and released; (3) “within-season recaptures” are recapture events that occurred within a single sampling season; and (4) “between-season recaptures” are recaptures that occurred after one or more seasons. As discussed below, analyses of growth and abundance were based largely on data for between-season recaptures.

For some analyses, we organized the capture-recapture data into six different spatial “strata” defined by river km (described below). These strata were arbitrarily selected to represent distinct sections of the study area and to provide reasonable sample sizes for comparisons among strata.

### *Adult Size and Growth*

Spatial and temporal patterns in size of captured adults were analyzed using length data. First, mean lengths of captures among strata were compared using analysis of variance (ANOVA). Data for four key strata were then pooled across consecutive 3-yr periods to examine potential changes in length distributions over time. This level of data aggregation provided reasonable sample sizes for comparing distributions. Mean lengths by period were compared using ANOVA, and linear regression was used to assess the time trend in annual estimates of mean length.

We used the capture-recapture data to estimate a tentative length-age relationship based on the “LVB” (you need to define “LVB” unless I missed it) growth model (Quinn and Deriso 1999):

$$L_i = L_\infty \left[ 1 - e^{-K(t_i - t_0)} \right] + w_i,$$

where  $L$  is the length of fish  $i$  at age  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is a growth parameter defining curvature, and  $t_0$  is interpreted as the age when an individual would have been length 0 had the growth model been operative at all ages. Errors  $w$  were assumed to be additive and normally distributed with mean zero and standard deviation  $\sigma_w$ .

For recapture data, the LVB model can be formulated as:

$$L_{2i} = L_\infty (1 - e^{-K\Delta t_i}) + L_{1i} e^{-K\Delta t_i} + w_i,$$

where  $L_1$  and  $L_2$  denote the lengths of fish  $i$  at capture periods 1 and 2, respectively, and  $\Delta t_i$  is the elapsed time (time as in years, months, days ?) between periods. In this formulation, only  $L_\infty$  and  $K$  can be estimated. To fully specify the length-age relationship, the value for  $t_0$  must be assumed or derived from auxiliary data (Quinn and Deriso 1999). We chose two values for  $t_0$  (0 and -1) based on inspection of length-age curves derived for six North American burbot populations (Katzman and Zale 2000). By projecting these curves backward, it appeared that most curves would have intersected the X-axis (zero length) between hypothetical ages 0 and -1. Parameters  $L_\infty$  and  $K$  were estimated via maximum likelihood (nonlinear least squares), and approximate standard errors and confidence intervals were derived using likelihood theory (do we have a citation?).

#### *Abundance Estimates*

Abundance and survival were estimated using variations of the Jolly-Seber model applied to between-season recapture data. Although there were more within-season recaptures than between-season recaptures, the former were deemed less useful for estimating abundance for two main reasons. First, 25 of the 45 within-season recaptures occurred in the 2001 sampling season at a single site (Ambush Rock and vicinity). The remaining within-season recaptures were sparsely distributed across sites and seasons, providing little data for use in closed-population models with repeated sampling such as the Schnabel method (Seber 1984). Second, because of the social nature of burbot, fish appeared to be attracted to a hoop net if another burbot was already present in the net, particularly in the case of males being attracted to a net that contained a female. This tendency, which was most obvious for 2001 Ambush Rock recaptures, can introduce bias and complicates estimation of capture probabilities (which likely differ among individuals because of apparent behavioral differences). In contrast, use of between-season recaptures provided a tentative framework for integrating different sampling sites and seasons, as well as for estimating annual (between-season) survival rates.

The standard Jolly-Seber model was designed for “open” populations subject to mortality (or permanent emigration) and recruitment (or immigration) (Seber 1984, p. 196). When capture and recapture events occur across multiple time periods, as in the burbot data set, the model permits estimation of period-specific capture probabilities ( $p_t$ ) and survival rates ( $\phi_t$ ). In turn, these parameters are used to estimate abundance ( $N_t$ ) and net recruitment ( $B_t$ ) by period. The

accuracy and reliability of estimates will depend on the number of recaptures and the degree to which assumptions of the model are met. In general, Seber (1984) suggests that at least ten recaptures per release period and per recovery period are required to provide reasonable estimates of  $p_t$  and  $\phi_t$ . For Kootenai burbot, however, the total number of between-season recaptures for a given release year or recovery year ranged from zero to a maximum of eight.

Given so few recaptures, the number of parameters in the model had to be reduced (e.g., Brownie et al. 1986). Eight alternative models were explored. In the first model (denoted the “no-effort” model), data were pooled across four key strata to maximize recaptures, and capture probabilities and survival rates were assumed to be constant across years, such that  $p_t = p$  and  $\phi_t = \phi$  for all  $t$ . This model had two parameters ( $p$ ,  $\phi$ ) to be estimated. (Estimates of abundance and recruitment were still available by year.) While a constant survival rate seems plausible, a constant  $p$  may be a poor assumption, especially given that effort differed appreciably among years. Thus, in the second model we assumed that annual capture probabilities were a function of total hoopnet effort ( $E_t$ ) (Seber 1984, p. 296):

$$p_t = 1 - e^{-qE_t}.$$

The catchability coefficient,  $q$ , was assumed to be constant over time. To more readily interpret parameter estimates, we scaled annual effort by the mean effort across years ( $\tilde{E}_t = E_t / \bar{E}$ ) and defined  $q$  as:

$$q = -\log(1 - \tilde{p}),$$

where  $\tilde{p}$  is the “average” capture probability or probability of capture at  $E_t = \bar{E}$ . Thus, the “effort” model also had two parameters ( $\tilde{p}$ ,  $\phi$ ). For simplicity, we use notation  $p$  rather than  $\tilde{p}$  when referring to the capture probability for an effort model.

In the remaining six models, data were divided into two groups. A potential problem with the above models is that capture probabilities were assumed to be identical across strata, yet sampling effort often differed markedly among strata. As discussed below, one stratum in particular had a distinct sampling history and few between-stratum recaptures, thereby indicating reasonable independence. We therefore treated this stratum and the remaining strata as two separate groups. Parameters were estimated either jointly or separately across the two groups as follows. In the first model, both groups were assumed to have the same capture probability ( $p$ ) and survival rate ( $\phi$ ) (two parameters). Second, groups were assumed to have the same  $\phi$  but

different capture probabilities ( $p_1, p_2$ ) across years (three parameters in total). Last, groups were assumed to have different survival rates ( $\phi_1, \phi_2$ ) as well as different capture probabilities (four parameters). We then repeated these analyses using models that incorporated hoopnet-effort data as described above.

Models were fit via maximum likelihood and compared using Akaike's information criterion (AIC) (Hurvich and Tsai 1989; Burnham and Anderson 1998). This criterion measures the relative support of alternative models based on their likelihoods and numbers of parameters. The model with the lowest AIC is considered the “best” model. In general, alternative models are considered to have strong, moderate, weak or very little support if their AIC values differ from the lowest by less than 2, 2 to 4, 4 to 7, or more than 7, respectively (Burnham and Anderson 1998). Unlike the standard Jolly-Seber model, there are no analytical formulas for computing standard errors for reduced-parameter models (Brownie et al. 1986). We therefore used likelihood theory to estimate approximate standard errors and confidence intervals for one selected model. For all models, estimates of annual abundance ( $N_t$ ) and net recruitment ( $B_t$ ) were summarized in terms for their averages across years and their linear trends over time. The latter was computed as the annual percent change relative to the average (e.g.,  $\text{slope}[N_t \text{ vs. } t] / \bar{N} * 100$ ). Finally, we examined several assumptions underlying the abundance models as discussed below.

### *Population Model*

We used a simple deterministic model to explore relationships between expected length-frequency distributions of adult burbot and biological parameters related to growth, survival, recruitment, and capture vulnerability. This analysis was motivated by the fact that burbot length data are likely the most reliable and potentially informative data for inferring reasonable bounds for basic biological parameters. In sum, the model projected age-specific abundances and lengths of consecutive cohorts over time and evaluated the congruency between observed and expected length distributions under different parameter assumptions.

The age-specific abundance ( $N_a$ ) in year  $t$  was modeled as  $N_{a,t} = \phi N_{a-1,t-1}$ , where the survival rate  $\phi$  was assumed to be constant across ages and years. Ages 3 through 12 were modeled with each cohort initiated at an arbitrary abundance (recruitment) of age-3 fish ( $N_3$ ). Age-specific length distributions were modeled using the LVB model described above, but with

the important distinction that ages were assumed known. Finally, age-specific selectivity (capture vulnerability) was modeled using a logistic function with selectivity increasing with age to an asymptote of one (Quinn and Deriso 1999):

$$s_a = 1 - \frac{1}{1 + e^{n_1(a-n_2)}}.$$

Here,  $n_1$  defines the slope of the selectivity curve and  $n_2$  is the inflection point or age of 50% selectivity.

Using this framework, we explored several scenarios in which survival and growth parameters were fixed and then selectivity parameters were crudely estimated to provide a reasonable agreement between observed and expected length distributions. Parameter values were obtained by minimizing the sum of squared differences between observed and expected length frequencies (ranging from 300 to 800 mm in increments of 10 mm). Further details of specific scenarios are provided below.

## **Results**

### **Summary of Adult Sampling**

Since 1993, considerable fishing effort has focused on Kootenai River burbot; additionally, several burbot have been captured during sampling targeting sturgeon (Table 2). Total captures and recaptures are summarized in Table 4. These data include burbot captured during IDFG winter burbot sampling, BCMWLAP winter sampling, and incidental catch during IDFG summer sturgeon sampling. Across years, there was a total of 403 capture events, from which 300 burbot were newly tagged and released. Of the remaining 103 capture events, 45 were within-season recaptures, 27 were between-season recaptures, and 31 were cases in which burbot were not tagged. None of the burbot tagged in the 1993-1995, 1997, and 2003 sampling seasons was recaptured in subsequent years (Table 4).

Hoopnet effort varied annually since 1993, but generally increased over time (Table 5 and Figure 2). Catch also increased until 2001, but then declined substantially. Catch per unit of effort (CPUE) was highly variable from 1993 through 1998, and declined steadily thereafter (Table 5 and Figure 2). Hoopnet effort and burbot captures were concentrated in three discrete areas within the Kootenai River: Goat River (rkm 152.7), Boundary Creek (rkm 170), and Ambush Rock (rkm 244.5; Figure 3).

**Table 4. Summary of annual adult burbot captures and recaptures in the Kootenai River, 1993-2004.**

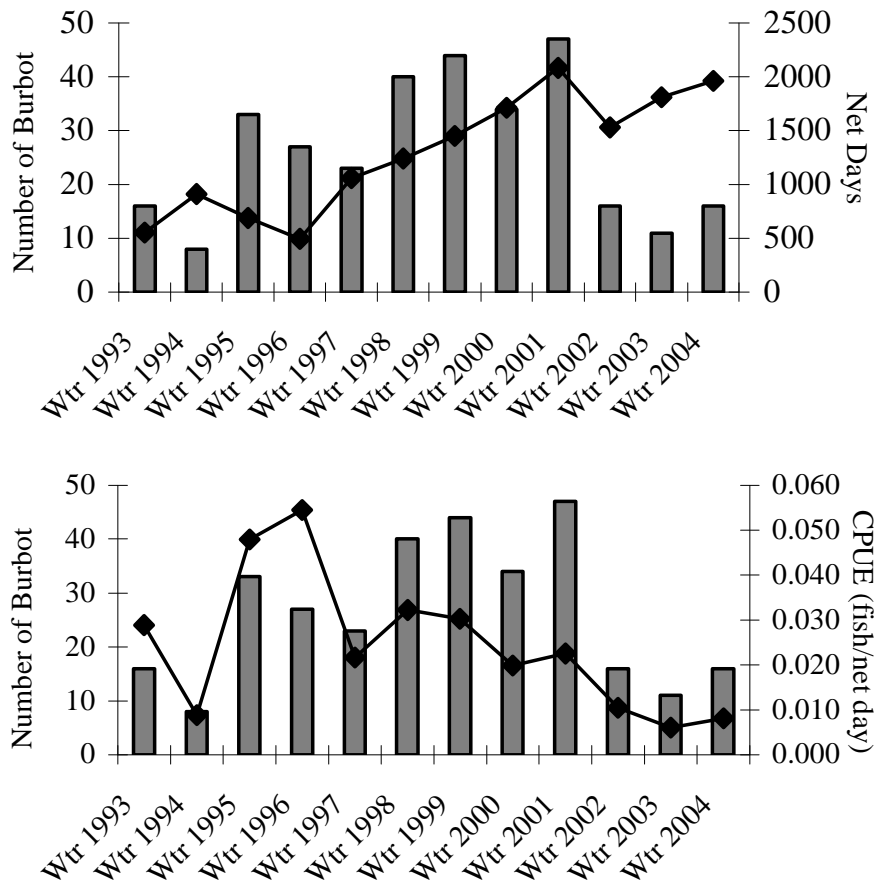
Year	Number of Burbot																	Recap %	
	Captured				Recaptured														
	Total Captured	New Tags	Between Season Recaps	Within Season Recaps	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	Total		
1993	17	15	0	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0%
1994	15	9	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0%
1995	33	20	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0%
1996	34	30	0	1	-	-	-	-	3	3	2	0	0	0	0	0	0	8	27%
1997	24	21	3	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0%
1998	59	50	3	3	-	-	-	-	-	-	1	0	0	0	0	0	0	1	2%
1999	47	40	3	2	-	-	-	-	-	-	-	1	1	0	0	0	0	2	5%
2000	36	31	1	3	-	-	-	-	-	-	-	-	-	7	2	0	1	10	32%
2001	74	40	8	26	-	-	-	-	-	-	-	-	-	5	0	1	6	15%	
2002	33	19	7	5	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0%
2003	11	10	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0%
2004	20	15	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Totals	403	300	27	45	0	0	0	0	3	3	3	1	8	7	0	2	27	9%	

Note: The year convention used in this table corresponds to the sampling year and NOT the calendar year. The sampling year began in the winter (roughly on November 1) and continued through the following spring (except for limited summer sampling in 1994 and 1996).

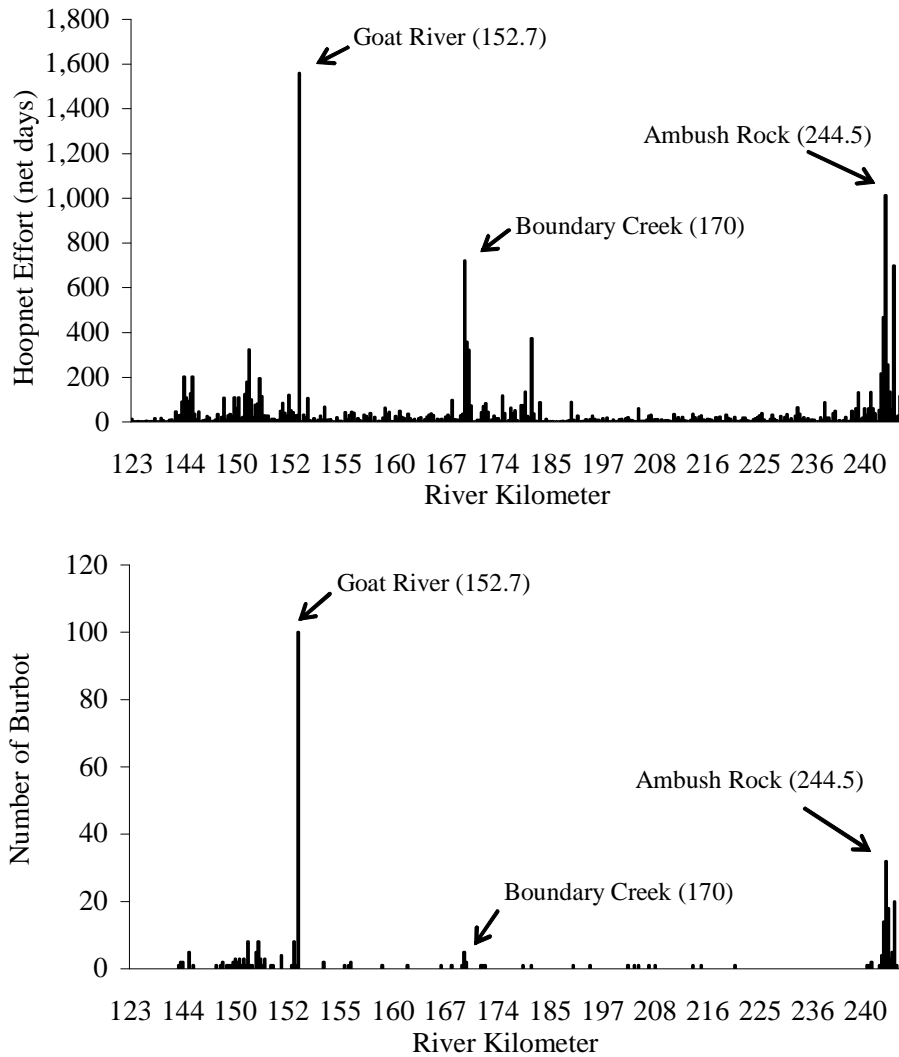
**Table 5. Kootenai River burbot catch, effort, and CPUE by sample season, 1993-2004 (IDFG winter hoopnet effort only).**

Sample season	Burbot Captures <sup>a</sup>	Total Hoopnet Days	CPUE (fish/net day)
Wtr 1993	16	554.2	0.029
Wtr 1994	8	909.8	0.009
Wtr 1995	33	688.8	0.048
Wtr 1996	27	495.8	0.054
Wtr 1997	23	1,061.1	0.022
Wtr 1998	40	1,240.9	0.032
Wtr 1999	44	1,453.7	0.030
Wtr 2000	34	1,712.9	0.020
Wtr 2001	47	2,085.2	0.023
Wtr 2002	16	1,529.9	0.010
Wtr 2003	11	1,809.7	0.006
Wtr 2004	16	1,965.1	0.008
<i>Total</i>	<i>315</i>	<i>15,507.1</i>	<i>0.020</i>

<sup>a</sup> Burbot captured in the same location during the same sampling season were not considered recaptures and were dropped from the analysis.



**Figure 2. Kootenai River burbot sampling effort and CPUE trends over time, 1993-2004 (IDFG winter hoopnet effort only). Note: Bars represent the number of burbot in each graph while the line represents the effort and CPUE in the top and bottom graphs, respectively.**



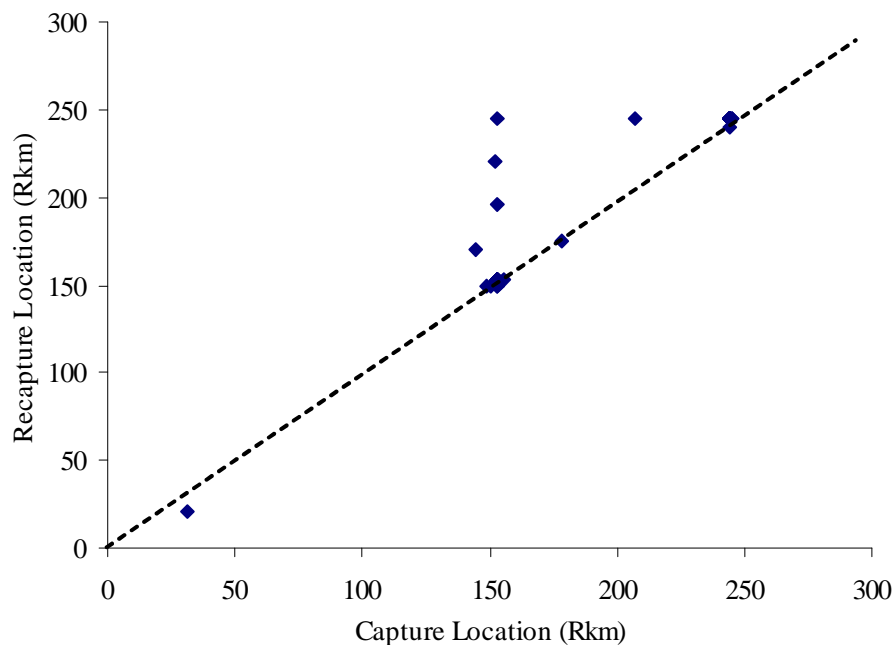
**Figure 3. Hoopnet effort and catch by river kilometer, 1993-2004 (includes only IDFG winter hoopnet effort).**

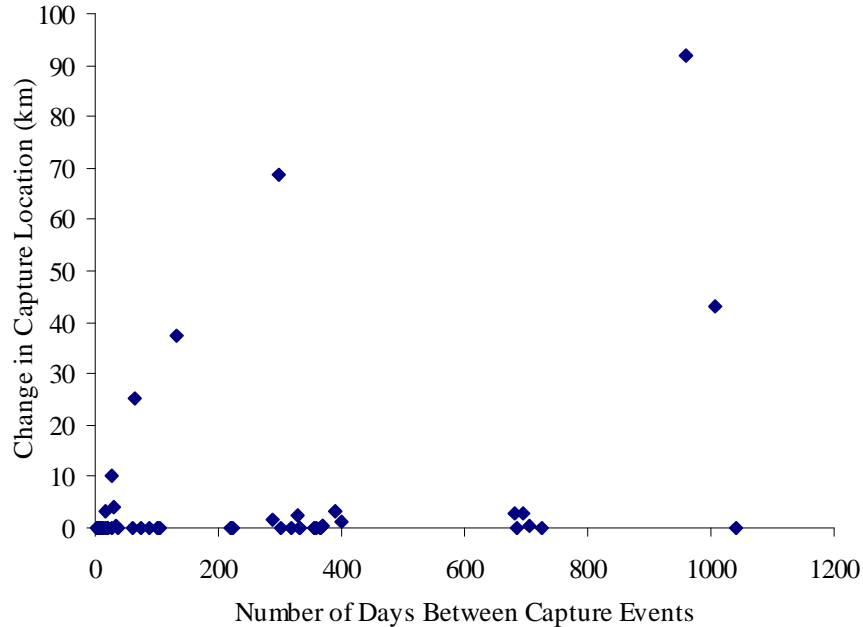
Data were divided into six spatial strata to facilitate analyses (Table 6). Stratum 1 represented data collected in Kootenay Lake; strata 2, 4 and 6 represented long sections of the Kootenai River (strata 6 was sampled in the 1993 winter season but little thereafter); and stratum 3 (Goat River) and stratum 5 (Ambush Rock and vicinity) represented key spawning locations. Although the majority of captures occurred in strata 3 and 5, more effort was devoted across years to strata 2 and 4 (Table 6).

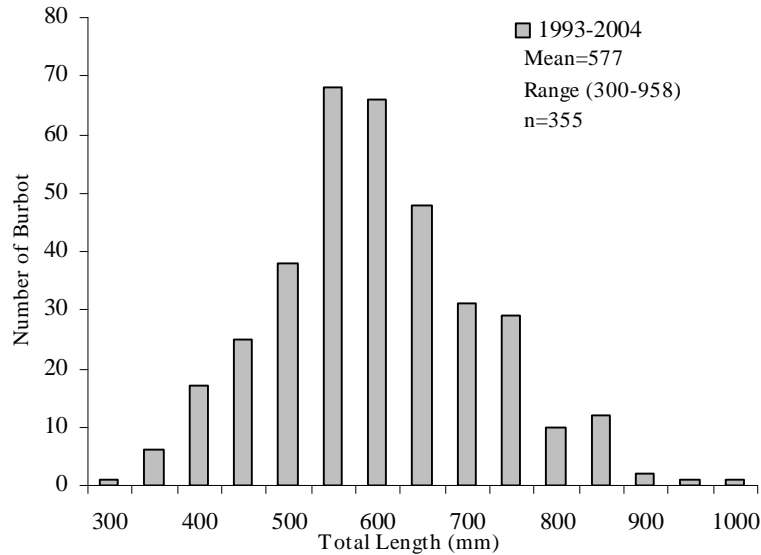
**Table 6. Kootenai River burbot capture data (across all gear types) by strata, 1993-2004 (IDFG winter hoopnet effort only).**

Stratum	RKM	Description	Hoopnet		Tagged	Recaptures	
			Effort	Captures		Within-season	Between-Season
1	15.7 - 121.9	Kootenay Lake	na	24	16	1	0
2	123.5 - 152.6	Kootenai River	3628	76	65	1	5
3	152.7	Goat River	1560	127	103	8	7
4	153.6 - 242.0	Kootenai River	7238	46	39	3	2
5	244.2 - 245.0	Ambush Rock	2896	129	76	32	13
6	249.4 - 270.0	Kootenai River	186	1	1	0	0
Totals				403	300	45	27

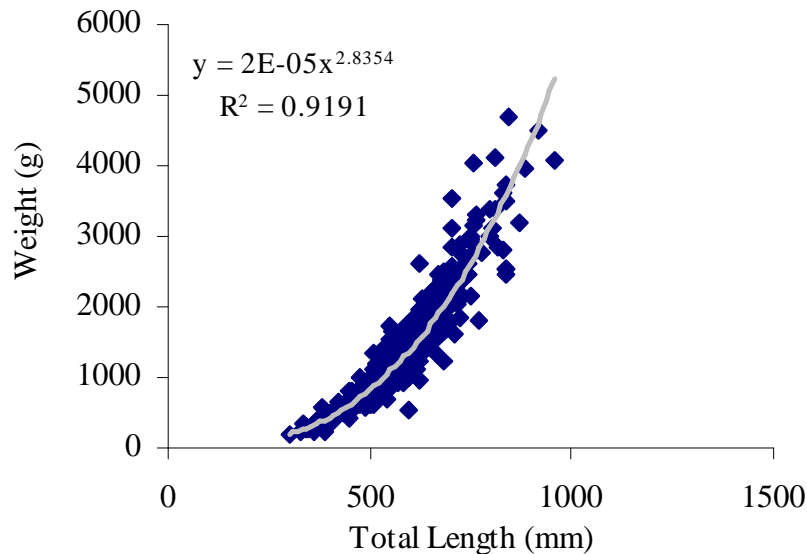
Burbot movement was tracked using data on recaptured fish (Note that IDFG has conducted annual burbot radio telemetry tracking to record fish movement; these data are summarized in the various IDFG annual progress reports to BPA and Paragamian 2000). Few burbot were recaptured at a location different than the initial capture location (Figure 4). Of those burbot recaptured at different locations, maximum distances traveled between capture locations approached 100 km. Duration between capture events at the same location was as long as 3 years (Figure 5).

**Figure 4. Comparison of initial capture location and location of recapture (dashed line represents no difference in capture and recapture location).**



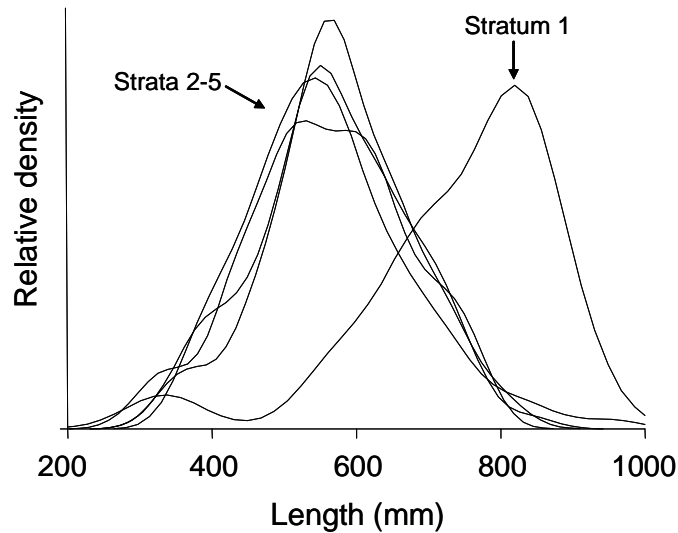


**Figure 6. Length-frequency distribution for burbot captures and recaptures, 1993-2004 (same season/location recaps removed from analyses).**

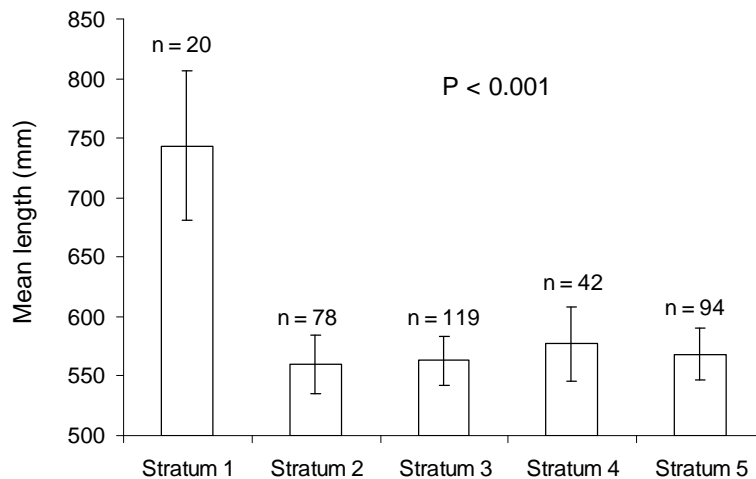


**Figure 7. Length-weight relationship for burbot captures, 1993-2004.**

There were obvious spatial and temporal differences in lengths of captured fish. Across all years, length distributions were remarkably consistent for strata 2 through 5, but fish captured in stratum 1 (Kootenay Lake) tended to be much larger (Figure 8). Mean lengths for strata 2-5 were similar (range: 560 to 577 mm), while the mean length for stratum 1 (743 mm) was significantly larger (ANOVA,  $P < 0.001$ ) (Figure 9).



**Figure 8. Length distributions (density functions) for burbot captures by strata, 1993-2004.**



**Figure 9. Mean lengths and 95% confidence intervals for burbot captures by strata, 1993-2004.**

Consequently, to analyze temporal trends in length, we omitted fish from stratum 1 because of their anomalous size and because most fish were captured in only two years (1996 and 1998). For the remaining data (pooled across strata 2 through 5), there was a clear trend toward larger lengths in later time periods. Length distributions for combined 3-yr periods showed subtle but important differences (Figure 10). For the first 3-yr period (1993-1995), there was an obvious “shoulder” in the distribution at lower lengths. In contrast, a similar shoulder existed at higher lengths in the final period (Figure 10). Differences in mean lengths for the four periods were highly significant (ANOVA,  $P < 0.001$ ) (Figure 11). In general, mean length increased by roughly 8 mm/yr on average from 516 mm in 1993 to 629 mm in 2004 (Figure 12).

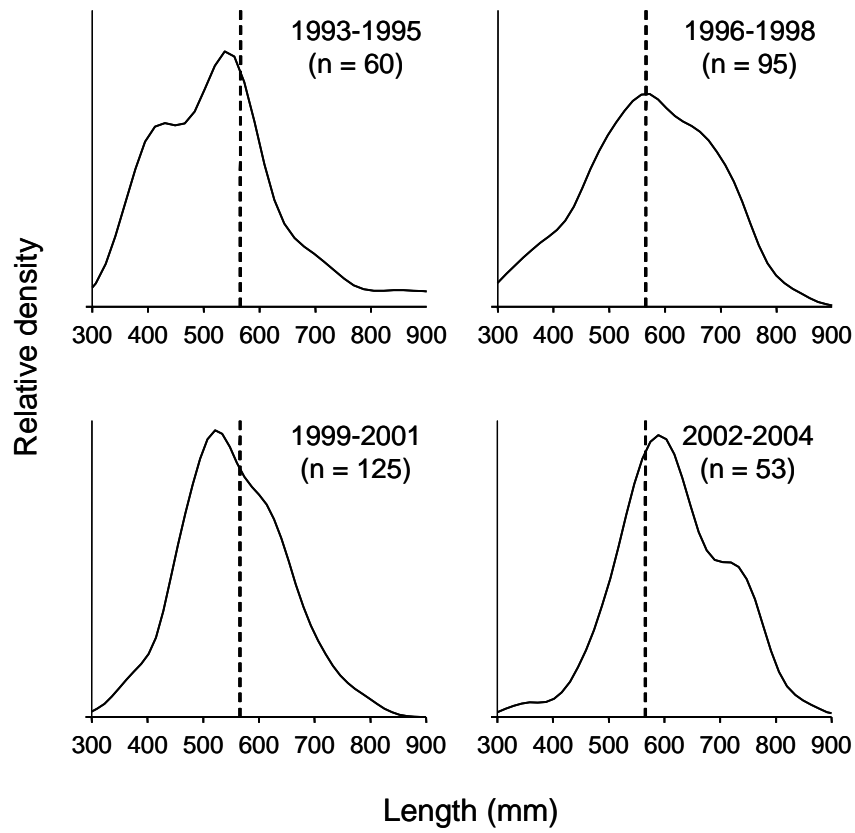


Figure 10. Length distributions by period for burbot captured in strata 2-5 (dashed line is the grand mean).

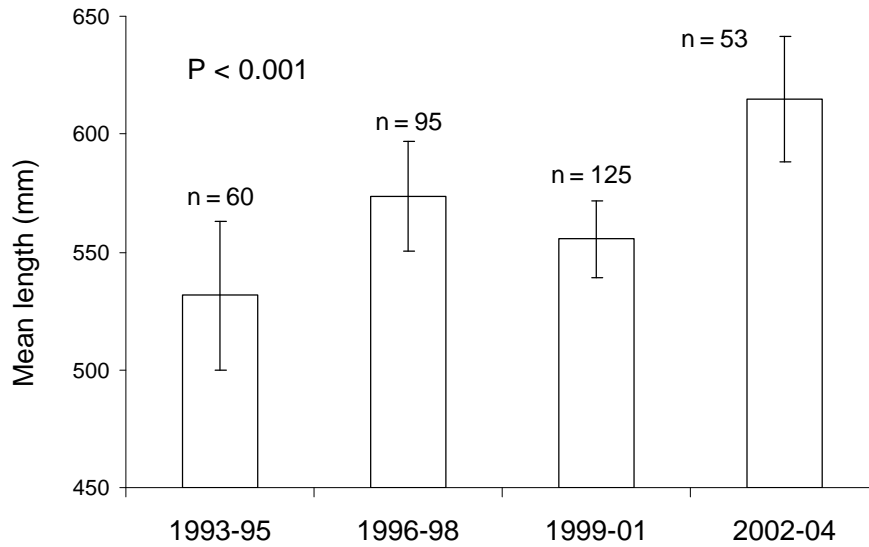
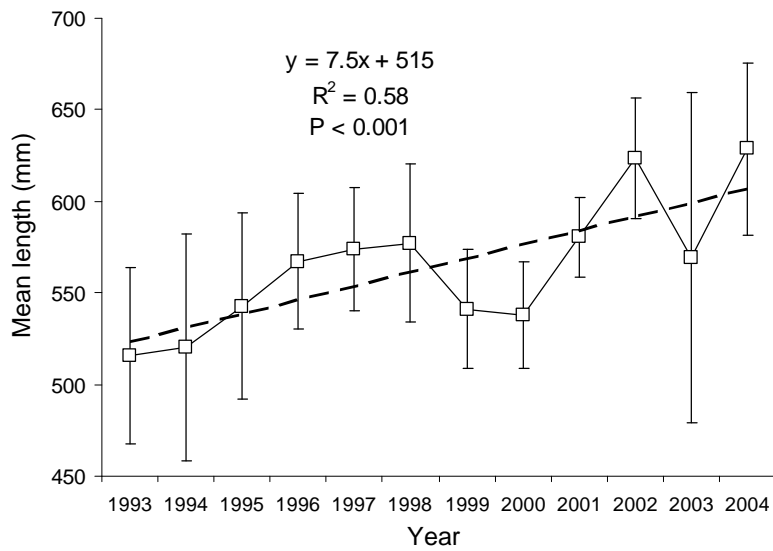
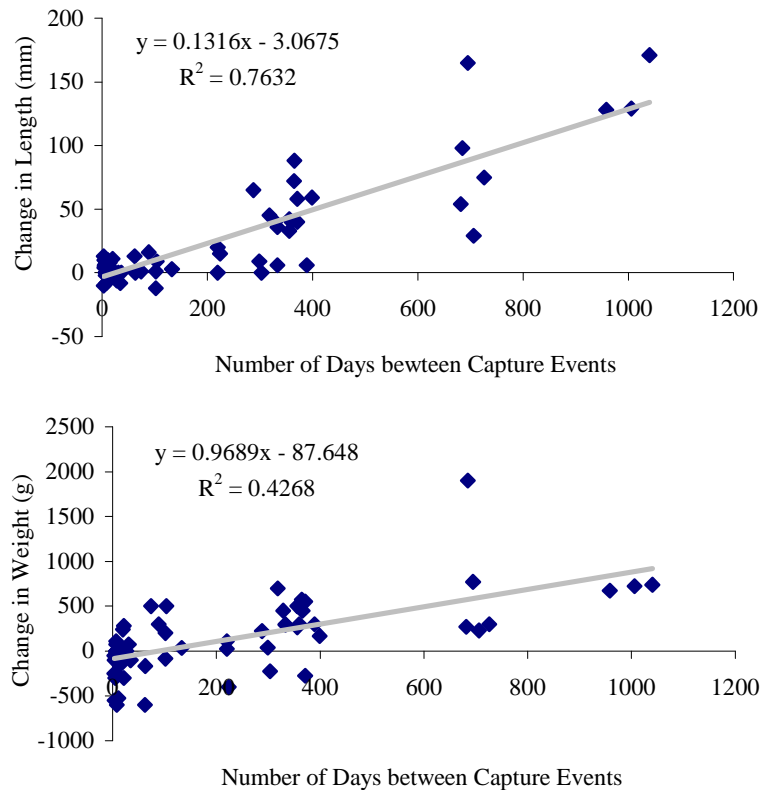


Figure 11. Mean lengths and 95% confidence intervals by period for burbot captured in strata 2-5.



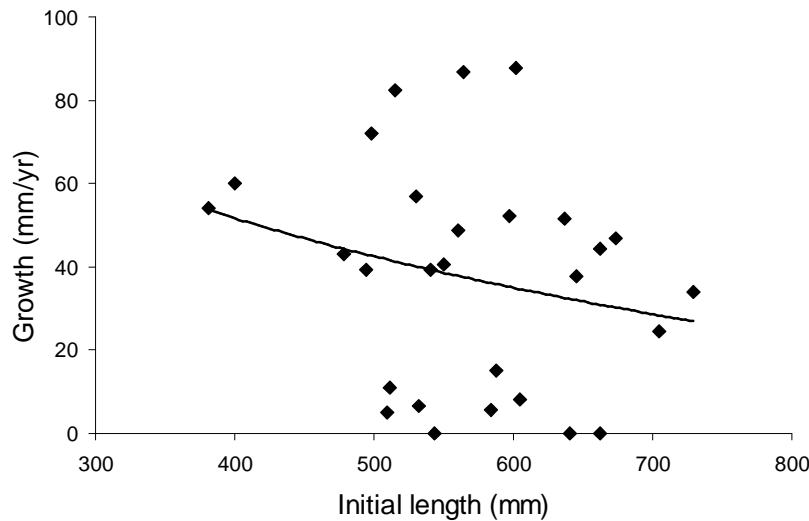
**Figure 12. Annual mean lengths and regression against year for burbot captured in strata 2-5.**

Growth of burbot (measured in both length and weight) was tracked using data for recaptured fish. Changes in length and weight were a function of time (Figure 13). In some instances, there was a negative change in length or weight over time; negative growth was measured more often using weight as a metric rather than length.



**Figure 13. Growth of recaptured burbot between capture events.**

We estimated tentative length-age relationships using data for 28 recaptures. Elapsed time between initial capture and recapture events ranged from 63 to 1040 days (median = 358), while observed annual growth increments ranged from 0.0 to 88 mm/yr (median = 40). Observed growth increments declined slightly as a function of initial length (Figure 14).



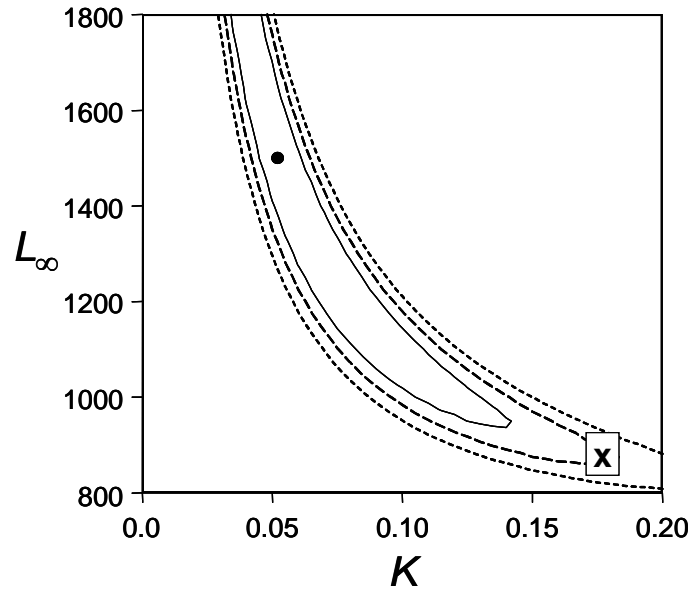
**Figure 14. Annual growth increments in length (mm/yr) for 28 recaptures.**

Parameter estimates for the LVB growth curve were highly uncertain (Table 7; Figure 15), yet provided sensible length-age relationships given assumed values of  $t_0$  (Figure 16). Both curves in Figure 16 are generally consistent with length-age relationships of other North American burbot populations, though at the low end (Katzman and Zale 2000). Across the six populations presented in Katzman and Zale (2000), mean lengths of age-1 fish range from roughly 100 to 200 mm, while lengths of age-10 fish range from roughly 600 to 800 mm, depending on the population. (Note that the “example” parameter combination in Figure 15 and growth curve in Figure 16 are discussed below in relation to the “Population Model.”)

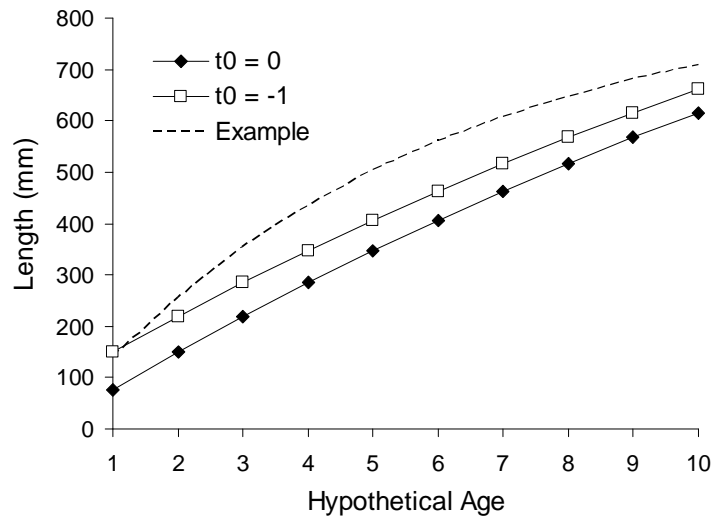
Of course, the curves in Figure 16 should be interpreted cautiously because they are based on assumed values of  $t_0$  and imprecise LVB estimates. In addition, growth curves based on recapture data have a somewhat different interpretation than standard size-age curves (where age is known) and may therefore result in different estimates (Quinn and Deriso 1999). Specifically, the recapture model estimates growth as a function of size rather than age. Also, the estimate of  $\sigma_w$  (28.3 mm) is properly interpreted as the standard deviation in annual growth rates across individuals, which incidentally is quite large (Figure 14), rather than as the standard deviation of lengths at a given age.

**Table 7. Parameter estimates and standard errors for the LVB growth model fit to length data for 28 capture-recapture events for Kootenai burbot.**

Parameter	Estimate	SE
$K$	0.052	0.047
$L_{\infty}$ (mm)	1517	834
$\sigma_w$ (mm)	28.3	



**Figure 15. Joint confidence regions (solid line: 80%; dashed line: 95%; dotted line: 99%) for parameters of the LVB growth model. “X” corresponds to parameters values for a hypothetical example.**



**Figure 16. Length-age curves based on the LVB model fit to recapture data for Kootenai Burbot. Curves are shown for two assumed values of  $t_0$  (0 and -1) and a hypothetical example.**

## Abundance Estimates

### *Combined-Strata Models*

Abundance and survival were first estimated using data pooled across strata 2-5 for sampling seasons 1996-2004. As noted earlier, none of the burbot tagged in the 1993-1995 seasons was recaptured during subsequent seasons, and hence these years were omitted from all analyses.

The “effort” model for the combined strata provided a slightly better fit (lower AIC) than the “no-effort” model, but both models provided similar parameter estimates (Table 8). Estimates of capture probability ( $p \approx 0.2$ ) imply that roughly 20% of the population was sampled on average, while estimates of  $\phi$  ( $\approx 0.4$ ) imply fairly low annual survival rates of roughly 40% on average. Averages of annual abundance ( $N_t$ ) and net recruitment ( $B_t$ ) estimates were roughly 150 and 90, respectively (Table 8). Abundance estimates for both models declined over time (Figure 17), though the average decline was greater for the effort model (14%/yr) than for the no-effort model (8%/yr; due primarily to the low abundance estimate in 2003). Larger declines were evident for recruitment estimates (Figure 18). In this case, the decline was greatest for the no-effort model (Table 8).

**Table 8. Parameter and abundance estimates for capture-recapture models (strata 2-5). Approximate 95% confidence intervals for parameters of the “effort” model are shown in parentheses.**

Model	AIC	$P$	$\phi$	Average		Decline (%/yr)	
				$N_t$	$B_t$	$N_t$	$B_t$
No effort	212.2	0.21	0.40	153	95	8%	27%
Effort	211.5	0.24 (0.12–0.41)	0.37 (0.24–0.50)	148	77	14%	21%

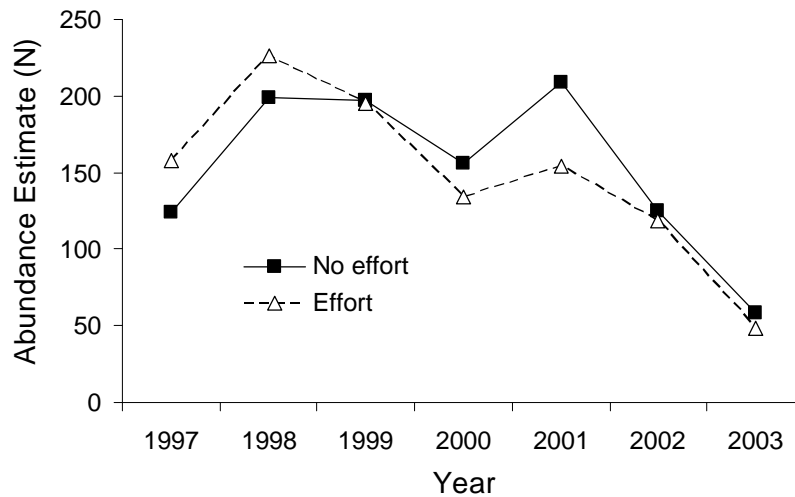


Figure 17. Estimates of Kootenai burbot abundance ( $N_t$ ) for capture-recapture models (strata 2-5).

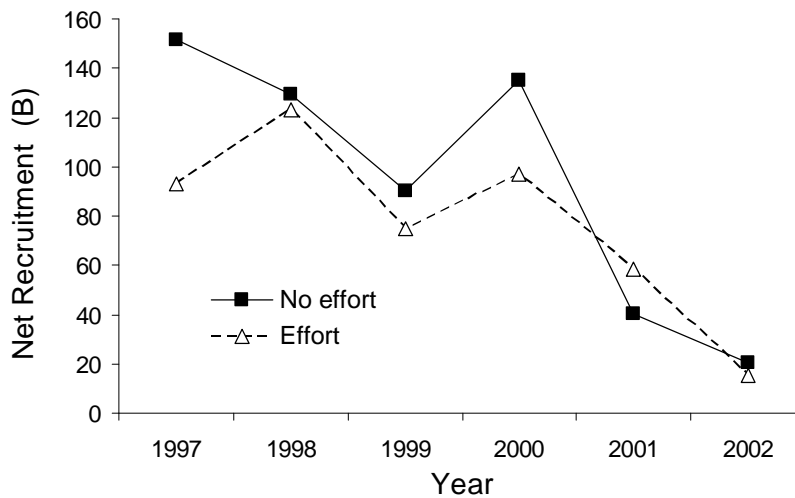


Figure 18. Estimates of Kootenai burbot recruitment ( $B_t$ ) for capture-recapture models (strata 2-5).

The precision of parameter estimates and implications for abundance estimates were explored for the effort model. The marginal 95% confidence intervals for each parameter and their joint confidence regions indicate considerable uncertainty (Table 8, Figure 19). Abundance estimates, however, were far more sensitive to changes in  $\hat{p}$  than  $\hat{\phi}$ . Figure 20 shows the average abundance estimate ( $\hat{N}$ ), integrated across  $\hat{\phi}$ , as a function of  $\hat{p}$ . The approximate 95% confidence interval for  $\hat{p}$  corresponded to a range of  $\hat{N}$  from 85 at  $\hat{p} = 0.41$  to 294 at  $\hat{p} = 0.12$  (Figure 20). Changes to either  $\hat{p}$  or  $\hat{\phi}$  essentially scaled all annual abundance estimates either

upward or downward, and hence, estimated declines in abundance ( $\approx 14\%/yr$ ) changed little across combinations of  $\hat{p}$  and  $\hat{\phi}$ .

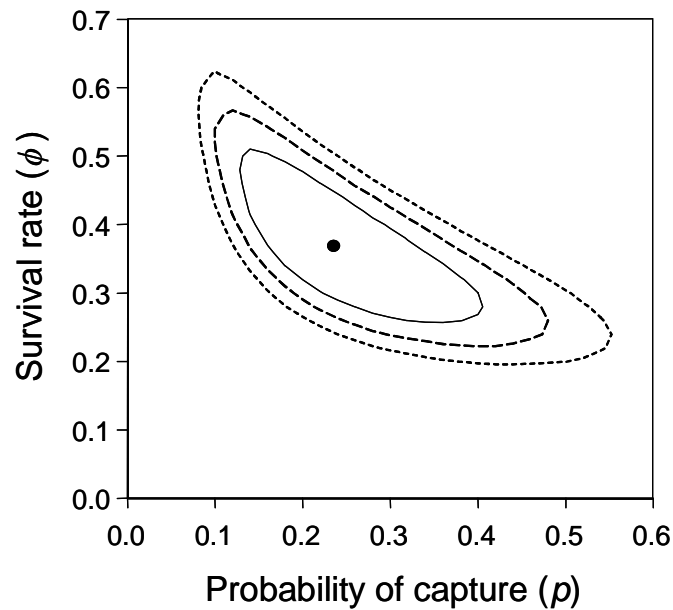


Figure 19. Joint confidence regions (solid line: 80%; dashed line: 95%; dotted line: 99%) for parameters of the “effort” capture-recapture model (strata 2-5, 1996-2004).

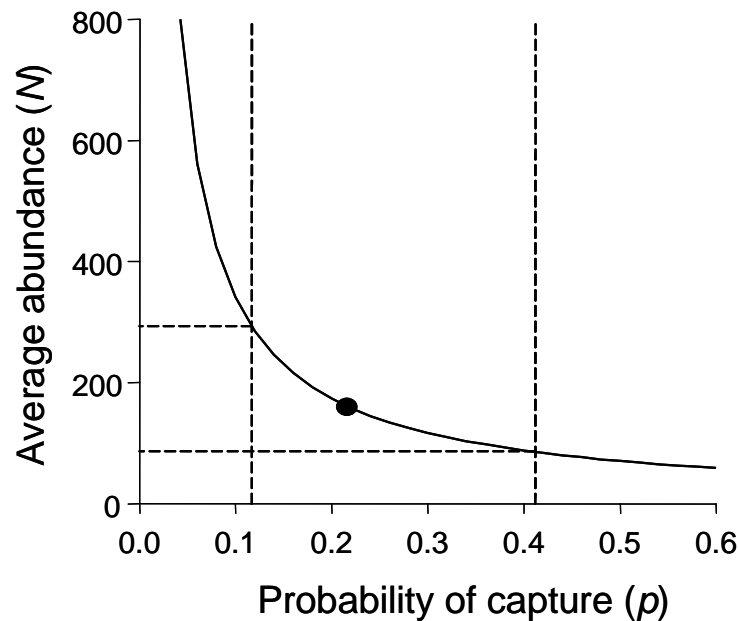


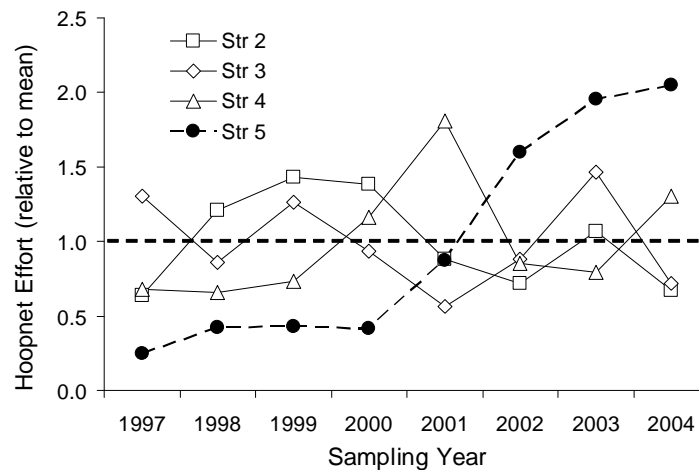
Figure 20. Estimates of average Kootenai burbot abundance (strata 2-5, 1997-2003) as a function of capture probability ( $p$ ) for the “effort” model. Dashed lines indicate the 95% confidence interval for  $p$  and the corresponding average abundances (integrated across  $\phi$ ).

### Two-Stratum Models

The above models assumed that all (living) fish had equal probabilities of capture across strata. However, neither fish nor sampling effort could be considered uniformly distributed. The most obvious discrepancies were for stratum 5 (Ambush Rock and vicinity). For example, all 11 burbot released from this stratum were also recaptured there, while only two fish released from other strata were recaptured in stratum 5 (Table 9). Greater mixing was apparent among strata 2-4 (Table 9). In addition, there was a large increase in hoopnet effort for stratum 5 after the 2000 sampling season, while effort varied less for strata 2-4 (Figure 21).

**Table 9. Total burbot recaptures partitioned by stratum of release and recapture (1996-2004).**

Release Stratum	Recapture Stratum			
	S 2	S 3	S 4	S 5
S 2	1		1	
S 3	4	6	1	1
S 4		1		1
S 5				11



**Figure 21. Variability in hoopnet effort by stratum (Str) and year. Annual effort was divided by the mean across years for a given stratum (dashed line at 1.0 indicates the mean).**

We therefore treated strata 2-4 and stratum 5 as separate groups in the “two-stratum” models, which required omission of the two stratum-5 recaptures not released in that stratum (Table 9). For effort-based models, the effort index for strata 2-4 was computed as a weighted average of their scaled indices (Figure 21), with arbitrary weights (1, 4, and 2, respectively) roughly reflecting the relative number of recaptures in each stratum (Table 9). However, variability in the effort index was minimal regardless of the weighting scheme, and hence results were robust to alternative weightings.

Results for the two-stratum models suggested that capture probabilities differed considerably between the two groups (Table 10). The no-effort models outperformed effort models based on AIC; however, in either case, the best model incorporated different capture probabilities ( $p_1, p_2$ ) and a common survival rate ( $\phi$ ) (Table 10, Models B and E). The estimate of  $p$  for stratum 5 was generally twice that for strata 2-4. The main consequence of differing capture probabilities was an overall increase in abundance estimates (Table 10). On average, total abundances ( $N$ ) were slightly greater than 200 for Models B and E. By comparison, average abundances for the combined-strata models were roughly 150 (Table 8). Models that allowed for different survival rates ( $\phi_1, \phi_2$ ) also performed well based on AIC (Table 10, Models C and F). These models suggested that both  $p$  and  $\phi$  were larger for stratum 5 than for strata 2-4.

Declines in total abundance for two-stratum models (Table 10) were similar to those for combined-strata models (Table 8). For example, abundance and recruitment estimates are shown in Figure 22 and Figure 23 for Model E. Abundances in strata 2-4 appeared to decline steadily after 1998, while abundances in stratum 5 increased until 2001 (Figure 22). The net result was a somewhat stable trajectory for total abundance until 2001, followed by a sharp decline. Declining trends in total recruitment for two-stratum models (Table 10) were largely driven by sharp declines after 2000 (Figure 23).

Finally, including effort influenced results primarily through stratum 5. In effort models, estimates of  $p_t$  for stratum 5 increased over time from roughly 0.1 to 0.5 in accordance with the strong trend in effort (Figure 21). Consequently, abundance and recruitment estimates for stratum 5 were sensitive to the use of effort (Table 10), though differences were subtle in comparison to the overall abundance or recruitment trends (Figure 22 and Figure 23).

**Table 10. Parameter and abundance estimates for the “two-stratum” capture-recapture models. Parameters with subscripts “1” and “2” correspond to estimates for strata 2-4 and stratum 5, respectively.**

Model	Effort	Parameters	AIC	$p$	$\phi$	Average $N$			Average $B$			Trend in $N$ (%/yr)			Trend in $B$ (%/yr)		
						S 2-4	S 5	Total	S 2-4	S 5	Total	S 2-4	S 5	Total	S 2-4	S 5	Total
A	No	$p, \phi$	198.1	0.22	0.37	105	41	147	51	46	97	-20	+24	-7	-27	-24	-26
B	Effort	$p_1, p_2, \phi$	192.8	0.13, 0.41	0.42	179	22	202	73	26	99	-20	+24	-15	-31	-23	-28
C		$p_1, p_2, \phi_1, \phi_2$	193.7	0.18, 0.33	0.34, 0.51	134	28	161	66	30	96	-20	+24	-12	-27	-27	-27
D	Effort	$p, \phi$	199.3	0.20	0.37	118	60	177	52	60	112	-20	+8	-10	-25	-37	-31
E		$p_1, p_2, \phi$	197.0	0.14, 0.34	0.40	174	35	209	69	35	104	-20	+9	-15	-27	-34	-29
F		$p_1, p_2, \phi_1, \phi_2$	198.3	0.18, 0.29	0.33, 0.46	135	41	176	63	39	102	-20	+9	-13	-24	-38	-30

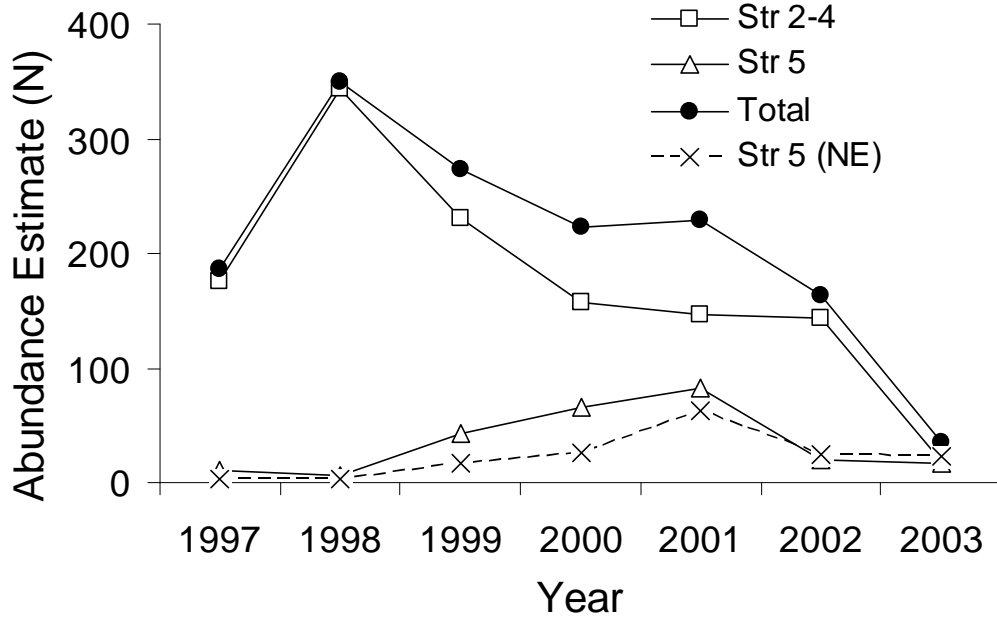


Figure 22. Estimates of Kootenai burbot abundance ( $N_t$ ) for Model E (effort). Also shown are abundance estimates for stratum 5 for Model B (no effort, NE).

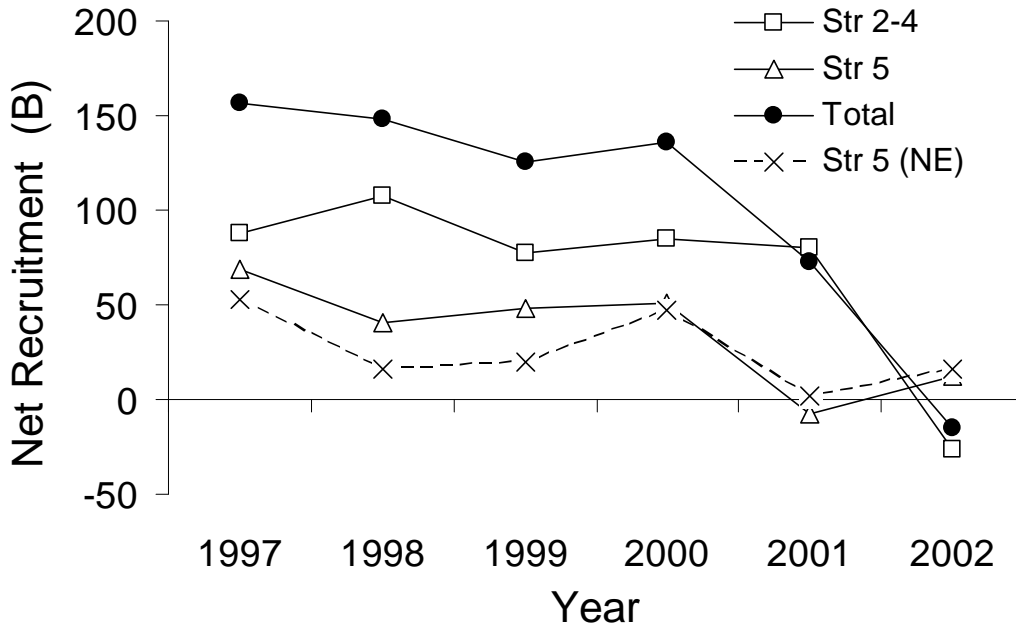


Figure 23. Estimates of Kootenai burbot recruitment ( $B_t$ ) for Model E (effort). Also shown are recruitment estimates for stratum 5 for Model B (no effort, NE).

*Validity of Assumptions*

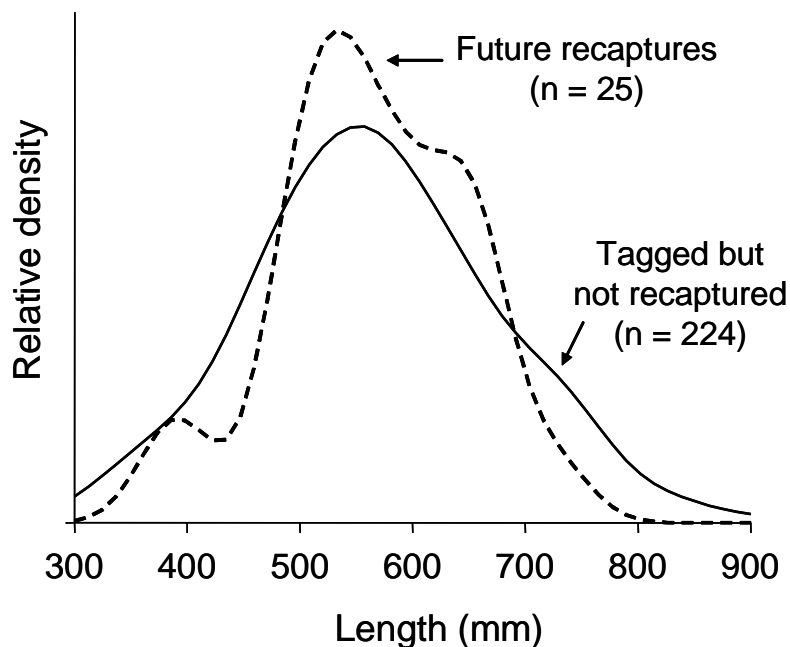
Several assumptions underlie the abundance and recruitment estimates of the above models (e.g., Seber 1984, p. 196): (1) every fish, whether tagged or untagged, has the same probability of capture either across all sampling seasons (no-effort models) or within a given sampling season (effort models); (2) every tagged fish has the same probability of surviving from one period to the next, and of a being present in the population during subsequent sampling periods; (3) tagged fish do not lose their tags and all tags are reported on recovery; (4) samples are instantaneous (sampling time is negligible); and (5) the survival rates of tagged and untagged fish must be the same for recruitment estimates to be valid.

Depending on the model, it was assumed that capture probabilities were equal across strata, across time periods, and/or proportional to sampling effort. Thus, assumption (1) was undoubtedly violated given that attributes of sampling (location, method, timing, intensity, and duration) varied considerably across strata and seasons. Assumption (2) is also questionable; the Jolly-Seber model allows for permanent emigration, but not temporary emigration. If burbot spawn intermittently (e.g., every two years) and are outside the sampling area in some years, then this assumption would be violated. It is unclear what effect this would have on abundance estimates. However, the sequence of between-season recaptures was consistent with consecutive spawning coupled with constant mortality (discussed below). Assumption (3) was likely satisfied. With respect to assumption (4), we used only between-season recaptures such that survival rates pertained to a period (roughly one year) greater than the sampling period. Across assumptions, violations of assumption (1) were likely the most serious. Nevertheless, results were generally consistent across models, including those with effort data and/or partitioned strata. So although we have limited confidence in any one annual estimate of abundance, it seems reasonable that overall averages and trends are reflective of historical conditions.

It is likely that tagged fish experienced greater mortality than untagged fish (assumption 5). Capture and handling of burbot resulted in ten reported deaths at the time of sampling, and two additional deaths were recorded within a few weeks of release. However, given so few recaptures it is not possible to directly test for immediate or sustained mortality due to tagging (Seber 1984, p. 230).

It is conceivable that relatively small fish experienced higher (delayed) mortalities due to capture and tagging, or that very large fish had high mortalities due to (implied) old age. To

asses evidence of size-dependent mortality, we compared lengths of fish that were tagged but not recaptured with fish recaptured one or more seasons later (Figure 24). The two distributions had similar means (565 mm in each case), but there were lower proportions of small and large fish among the recaptures (Figure 24). As a result, the length distribution for recaptures had a lower standard deviation (84 mm vs. 111 mm), which was marginally significant ( $P = 0.02$  and  $0.05$  for one-tailed and two-tailed F-tests, respectively). While this is consistent with hypotheses that relatively small or large fish experience higher mortality, it is difficult to draw a firm conclusion or speculate on mechanisms given the small sample size for recaptures.



**Figure 24.** Initial length distributions for burbot tagged but not recaptured (solid line) and burbot recaptured after one or more seasons (dashed line) (strata 2-5, 1993-2003).

Numerous captures were implanted with sonic tags in addition to PIT tags. We hypothesized that additional stress due to surgical implant of sonic tags would increase mortality and therefore reduce recapture rates. From 1993 to 2003, 77 of 268 PIT-tagged burbot also received sonic tags (29%), but only two of the 24 between-season recaptures had received sonic tags (8%). A simple binomial test suggests this recapture rate for sonic-tagged burbot was significantly lower than expected by chance alone. However, this test does not incorporate obvious differences among strata in recaptures rates and proportions of sonic-tagged burbot (most sonic tags were implanted in captures from strata 2 and 4). We therefore analyzed data for

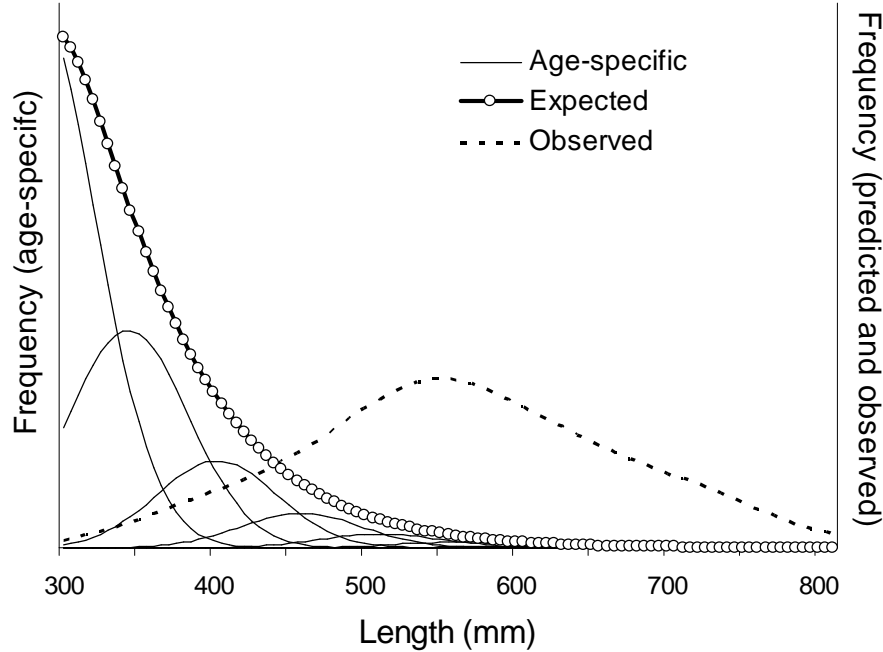
strata 2-5 in separate 2 x 2 contingency tables, and assuming independence among strata, summed the chi-square values (Seber 1984). Although the recapture frequency of sonic-tagged fish was lower than expected in all strata, the overall P-value was 0.07. Again, the evidence was merely suggestive.

Estimates of survival rate ( $\phi$ ) for the above models generally reflect the numbers of recaptures observed 1 to 4 seasons after last capture, which were 19, 5, 3, and 0, respectively. This sequence is consistent with consecutive spawning events (or persistence in the sampling area) and a survival rate of about 40%. However, a survival rate of 40% is not consistent with observed length distributions (discussed below), and more generally, with expected longevity of burbot. For example,  $\phi = 0.4$  implies an average life-span ( $= -1/\log[\phi]$ ) of approximately 1 year from the time of capture (Seber 1984, p. 216). When survival of tagged fish is not representative of the general population, estimates of recruitment ( $B$ ) are invalid. Here, we expect that estimated survival was low, and hence recruitment biased high.

### **Population Model**

Initial parameters for the population model were based on empirical estimates from the growth and capture-recapture models. Specifically, LVB parameters were set at  $K = 0.05$ ,  $L_\infty = 1500$ ,  $t_0 = -1$ , and  $\sigma_w = 0.5$ . In this case,  $\sigma_w$  reflects the standard deviation of lengths at a given age, which was assumed to be greater than the estimate for individual growth rates (Table 7). The survival rate ( $\phi$ ) was set at 0.4, and by default, all ages were assumed to have equal capture vulnerability (no selectivity). The observed length distribution, which the model attempted to approximate, was based on all captures for strata 2-5 (mean = 566 mm and SD = 108 mm).

The expected length-frequency given the initial parameter values was skewed strongly toward low lengths (Figure 25). This is easily anticipated. Under constant recruitment, there will be more fish in younger age classes. Thus, to approximate the symmetry of the observed distribution, relative capture vulnerabilities of younger fish must be reduced. However, it is also evident that few fish were expected to obtain lengths greater than 500 mm (Figure 25). In fact, there was no reasonable selectivity curve to reproduce the observed length distribution given the initial growth and survival parameters.

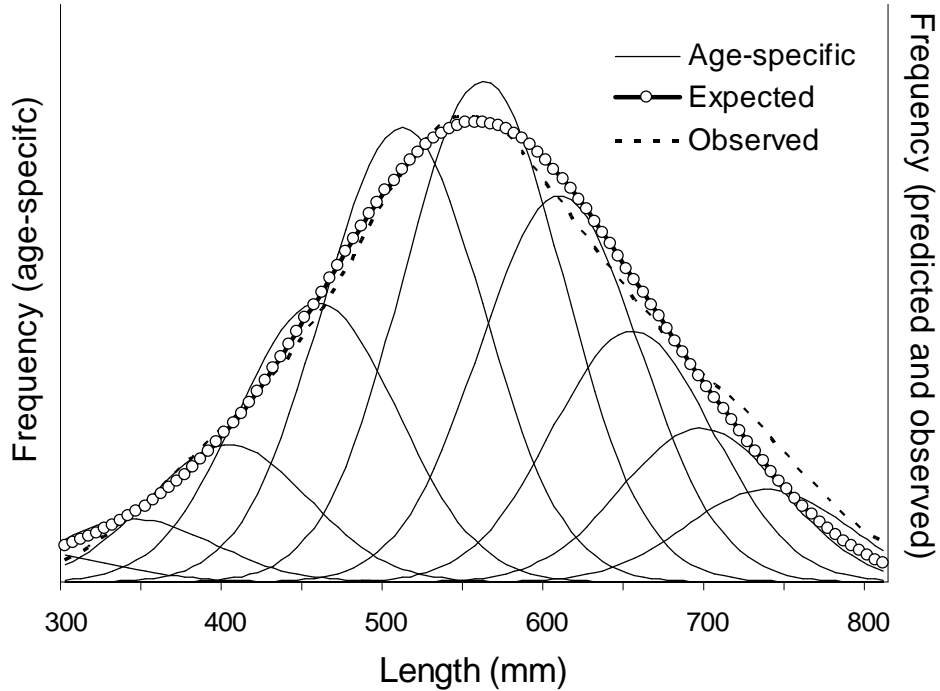


**Figure 25.** Length-frequency distributions (relative densities) for initial parameter values of the population model. The “expected” distribution integrates across age-specific distributions.

We present three scenarios in which growth and survival parameters were changed, and then selectivity parameters ( $n_1$  and  $n_2$ ) were crudely estimated (Table 11). First, we increased the survival rate ( $\phi$ ) to 0.6, a value at the upper bound of confidence region presented in Figure 19. Estimates of selectivity parameters were roughly  $n_1 = 1.3$  and  $n_2 = 7.4$  (Table 11, Case 1), providing a reasonable approximation of the observed length distribution (Figure 26). However, this implied a slow increase in selectivity with fish at age  $\approx 7$  (mean length = 529 mm) having a 50% capture vulnerability. Across ages 3-12, the vulnerable proportion of the population was only 17% (Table 11, Case 1).

**Table 11.** Parameter values for different scenarios of the population model. Also shown are mean lengths at age  $n_2$  (age of 50% vulnerability) and the vulnerable proportion of the population (ages 3-12).

	$K$	$L_\infty$	$t_0$	$\phi$	$n_1$	$n_2$	Length at $n_2$	% Vulnerable
Case 1	0.05	1500	-1	0.6	1.3	7.4	529	17%
Case2	0.18	850	0	0.4	1.5	6.0	561	18%
Case 3	0.18	850	0	0.6	1.5	5.0	507	51%
Case 4	0.18	850	0	0.6	2.5	4.0	436	78%, 89%



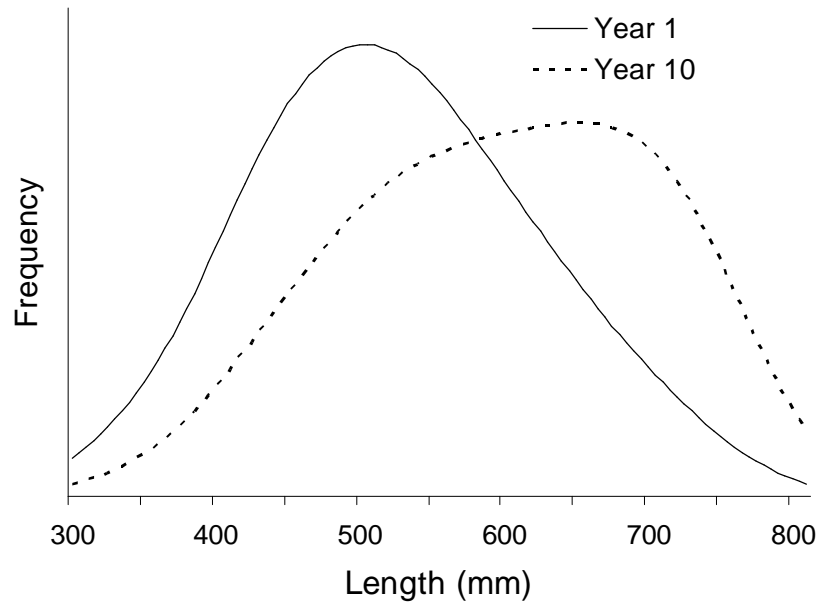
**Figure 26. Length-frequency distributions given parameter values for Case 1 (see Table 11).**

In the second scenario, LVB parameters were changed to  $K = 0.18$ ,  $L_{\infty} = 850$ , and  $t_0 = 0$  (with  $\phi$  set back to 0.4). These parameters imply more rapid growth, and correspond to the “example” parameter combination in Figure 15 and growth curve in Figure 16. (This growth curve is very similar to that presented in Katzman and Zale (2000) for burbot from Lake of the Woods, Ontario, in the mid range of the populations.) Again, however, the corresponding estimates for  $n_1$  and  $n_2$  implied very low capture vulnerabilities across ages (Table 11, Case 2).

The third scenario included both increased survival and growth rates, which yielded a more reasonable selectivity curve (Table 11, Case 3). The age of 50% capture vulnerability was 5 (mean length = 507 mm) and the vulnerable proportion of the population increased to 51%.

Last, we present a scenario in which recruitment ( $N_3$ ) declined over time. The goal here was to roughly mimic the observed increase in mean length over time (Figure 12) via a simple exponential decline in recruitment. Again, high survival and growth rates were assumed, as well as a steeper selectivity curve (Table 11, Case 4). A large decline in recruitment was required to produce a shift in the length distribution similar to the observed shift. For example, a 30% decline per year resulted in a change in mean length from about 530 mm in year 1 to 600 mm in year 10 (Figure 27). Recruitment and total abundance in year 10 were only 4% and 10% of that

in year 1, respectively. Interestingly, the decline and corresponding shift in age distribution allowed for greater capture vulnerabilities among younger age classes (age of 50% capture vulnerability was 4 with mean length = 436 mm). Consequently, for this scenario the vulnerable proportion of the population was 78% in year 1 and 89% in year 10.



**Figure 27. Expected length-frequency distributions in year 1 and 10 given an annual decline in recruitment of 30% with parameter values for Case 4 in Table 11.**

## ***Discussion***

Analyses of 12 years of capture-recapture data indicate confirm that burbot numbers are very low, numbers are declining, recruitment is poor, and the population is on the threshold of extinction. This conclusion is supported by annual abundance and recruitment estimates, declining CPUE in population surveys, and an increasing trend in average fish size.

Average estimates of adult burbot abundance for 1997-2003 ranged from 150 to 200, depending on the model. Although these estimates were based on few recaptures and simplifying assumptions, they seem reasonable in several respects. For example, 12 years of sampling produced only 403 captures, of which 72 were recaptures. In recent years, there were fewer than 30 captures annually despite high sampling effort. Uncertainty in the average abundance estimate was quantified for only one model, though this result should be generally applicable and suggests a rough confidence interval from one half to double the estimate. Of course, abundance estimates pertain only to the vulnerable portion of the burbot population in sample strata 2-5. For this reason, population estimates are likely conservative.

Catch rates for Kootenai River burbot are near the low end of values reported in other areas. Kootenai River CPUE ranged from 0.054 fish/net d in 1996 to a low of 0.008 fish/net d in 2004. Although gear types differed, the Kootenay Lake Balfour fishery CPUE was between 0.50 and 1.48 fish/hour (Redfish Consulting 1998). By comparison, CPUE in the Tanana and Chena rivers, Alaska, was greater than 1 fish/net day and 0.5 fish/net day, respectively (Evenson 1993). CPUE of burbot in four Alaskan Lakes ranged from 0.5 to 3.0 fish per net day (Parker et al. 1988).

Consistent capture of burbot occurred in only a few distinct areas: Ambush Rock, Idaho and in or near the Goat River, B.C. This occurred despite attempts to distribute effort uniformly. These locations may represent significant spawning locations. During the winter of 2000-2001, we captured over 20 burbot at Ambush Rock; both male and female burbot were identified as gravid, flowing, or spent. The highest catches of burbot in the Goat River occurred during this same time period and both gravid and spent fish were observed (Paragamian 1994a, 1994b; Paragamian 1995, 2000; Paragamian and Whitman 1996, 1997, 1998; Kozfkay and Paragamian 2002). There is no evidence of burbot spawning in other areas of the Kootenai River from Kootenay Lake to the Idaho-Montana Border.

Although there appears to be limited burbot movement between initial capture and recapture locations (Figure 4), these data may be misleading. Knowing the location of burbot at two discrete points in time, particularly when the time between capture and recapture is long, provides little information regarding movement patterns between capture events. Analysis of the capture and recapture locations is, however, suggestive of considerable site fidelity in Kootenai River burbot. In many cases, burbot were captured at the same location over multiple years, particularly in the Goat River and Ambush Rock areas.

Although burbot spawning and recruitment has been documented, observed declines in adult abundance and the general lack of small burbot (e.g., < 500 mm) in recent years indicate that recruitment rates are too low to sustain a significant population. Our simple burbot population model suggest that estimated recruitment estimates from the capture-recapture model were biased high. In the population model, dramatic declines in recruitment were needed to reproduce a shift in the length distribution similar to that observed. The specific causes of poor recruitment are unclear – the relative significance of spawning stock limitation and poor incubation and survival conditions are unknown.

Length-frequency distributions of captures suggest reasonable growth estimates of adult burbot in the Kootenai River over the period 1993-2004. Burbot can be caught in hoop nets at about 350 mm TL but are not fully recruited until 450 mm TL (Bernard et al. (1991). The length distribution of burbot across 1993-2004 (Figure 6) was similar to that of burbot harvested in the Balfour fishery in Kootenay Lake from 1968-1975 (Redfish Consulting 1998). Although the most common length of Kootenai River burbot was between 500 and 600 mm, compared to 650 to 750 mm for the Balfour fishery, there still were substantial numbers of burbot > 700mm captured since 1993. Furthermore, the population model indicated that growth rates consistent with the mid-range of burbot populations reported in Katzman and Zale (2000) were needed to reproduce observed distributions (conditional on a constant adult survival rate of 60% and a reasonable selectivity curve). For this growth curve, lengths of 500 to 600 mm were dominated by ages 5 to 7. Lower growth rates would necessitate higher survival rates, and would result in older fish in these length classes.

In contrast, survival rates were unreasonably low. Capture-recapture estimates of a 40% annual survival rate are not consistent with observed length distributions and estimated

individual growth rates. Such discrepancies may be because of sampling error, or may reflect adverse effects of capture, handling, and tagging on adult burbot.

These results indicate that the Kootenai River burbot will become extinct within the next decade and may already be past the point where recovery is feasible. Theoretical conservation biologist and geneticists estimate that a minimum effective breeding population ( $N_e$ ) of at least 50 to 500 individuals is necessary to sustain a viable population (Soule 1980; Lande and Barrowclough 1987). Genetic and demographic risks and uncertainties of smaller numbers are very high. Genetic risks include the potential loss of rare alleles, drift in gene frequencies, increased genetic load from inbreeding, and a small population founder effect in the next generation. Demographic risks include too few spawners to take advantage of suitable habitat conditions, if they occur.

The acute status of the Kootenai population presents some difficult choices for burbot conservation and recovery efforts. Current voluntary efforts to maintain low winter flows, thought to be conducive for burbot migration and spawning, have failed to arrest population declines or to restore significant burbot recruitment. It is unclear whether this failure results because flow measures fell short of necessary levels, recruitment is not flow limited, or other physical or biological changes in the system have rendered flow effects moot. Even if suitable habitat conditions can be immediately restored, recovery of the small remnant population may be precluded by genetic and demographic bottlenecks. Capture and artificial propagation of the last few wild individuals might be an option but effective burbot propagation methods have yet to be developed. Supplementation or reintroduction of burbot from other healthier populations is yet another alternative but non-native stocks might fare poorly and speed extinction of the locally-adapted native population. Without diagnosis and restoration of suitable habitat conditions for burbot, all conservation, recovery, or reintroduction measures are likely to meet with limited success. Finally, the value of additional burbot sampling activities may be questionable past the point of diminishing returns on new information gained.

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