

# Population Dynamics and Extinction Risk of Burbot in the Kootenai River, Idaho, USA and British Columbia, Canada

VAUGHN L. PARAGAMIAN\*

*Idaho Department of Fish and Game*

*2885 Kathleen Avenue, Coeur d'Alene Idaho 83815, USA*

BRIAN J. PYPER, MICHAEL J. DAIGNEAULT, AND RAYMOND C. P. BEAMESDERFER  
*Cramer Fish Sciences, 600 NW Fariss Road, Gresham Oregon 97030, USA*

SUSAN C. IRELAND

*Kootenai Tribe of Idaho, Post Office Box 1269, Bonners Ferry, Idaho 83805, USA*

**ABSTRACT.**—We examined the status and population characteristics of Kootenai River burbot *Lota lota* using capture–recapture data from 1993 to 2004. Our objective was to determine when this population may become functionally extinct and to help guide conservation efforts. A total of 403 burbot were captured, of which 300 were tagged and released, 31 were not tagged, and 72 were recaptures of fish tagged up to 4 years prior. Hoop-net catch per unit effort, where one unit of effort is a hoop-net set for 24 h, declined from 0.054 in 1996 to 0.008 in 2004. Mean total length of sampled burbot increased at a rate of about 8 mm/year from 1993 (516 mm) to 2004 (629 mm). Two models were developed for capture–recapture analysis, one that included effort data through a series of river reaches and one without effort data. The effort model appeared to be more reliable and suggested an average annual mortality rate for adult burbot (>250 mm) 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 have already reached functional extinction. We conclude that immediate remedial measures must be implemented by focusing on rehabilitation of the native genetic stock and habitat remediation described in other studies.

## Introduction

Burbot *Lota lota* are the world's only freshwater species of the family Gadidae and only one of two species of freshwater fish that have a circumpolar distribution (McPhail and Lindsey 1970). Even with this broad

distribution, burbot population dynamics are not well described, and in many waters, they are lacking in comprehensive management (Paragamian and Willis 2000). One reason is because, in many areas, burbot are held in low esteem, yet in others, they are the subject of special fishing events (Quinn 2000). Although burbot are widespread and abundant throughout much of their natural range (Muth

\* Corresponding author: vparagamian@idfg.idaho.gov

and Smith 1974; Bruesewitz 1990; Evenson and Hansen 1991; Edsall et al. 1993), there are many populations that have been extirpated or are in serious decline (Maitland and Lyle 1990; Keith and Allardi 1996; Maitland and Lyle 1996; Argent et al. 2000; Arndt and Hutchinson 2000; Paragamian et al. 2000).

The Kootenai River in Idaho, USA and British Columbia, Canada and Kootenay Lake are near the southern edge of the burbot distribution in North America (Figure 1; McPhail and Lindsey 1970). The Kootenai River burbot population is in serious decline because of habitat alterations and construction of Libby

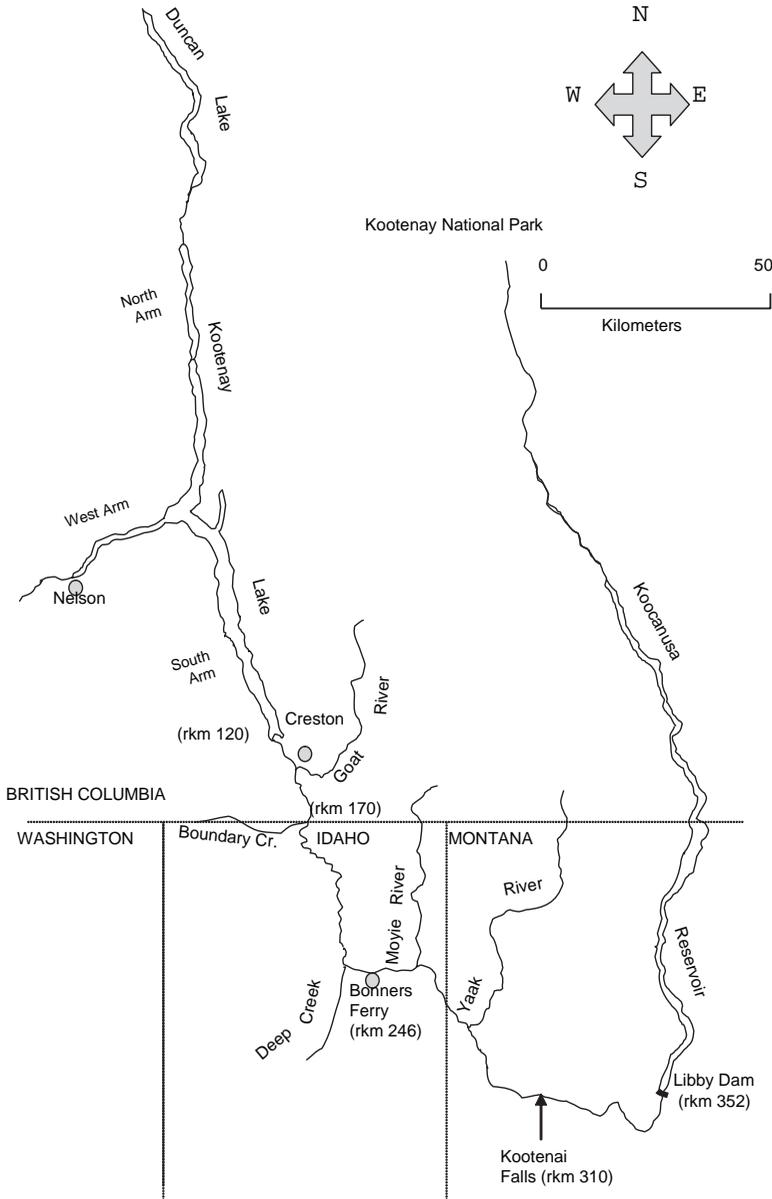


FIGURE 1. Location of Kootenay Lake, the Kootenai River, Lake Koocanusa, and major tributaries in the basin. River kilometer measurements are from the northernmost arm of Kootenay Lake.

Dam near Jennings, Montana by the U.S. Army Corps of Engineers in 1972 (Paragamian et al. 2000; Anders et al. 2002). Popular burbot fisheries in Kootenay Lake, British Columbia and the Kootenai River, Idaho had collapsed by the late 1970s (Paragamian et al. 2000). Neither population has recovered despite closure of the fisheries (Paragamian et al. 2000).

Lake, river, and tributary spawning by burbot in the Kootenai River and Kootenay Lake were represented, but recruitment appears to have failed for all three life histories. Burbot remain in Duncan and Trout lakes in the northern drainage into Kootenay Lake, but burbot are now rarely observed in the south or west arms of the lake or the river between the lake and Kootenai Falls, Montana, USA. Burbot remain common in the upper Kootenai River system upstream from Kootenai Falls, including Libby Reservoir and the upstream river (J. Dunnigan, Montana Fish Wildlife and Parks, personal communication). Mitochondrial DNA studies have shown that burbot in the lower Kootenai River in Idaho and British Columbia and Kootenay Lake are genetically different from burbot stocks in Montana upstream of Kootenai Falls (Paragamian et al. 1999; Powell et al. 2008, this volume; Figure 1).

Burbot represent a significant historical and cultural resource to the local region and are the subject of a regional burbot conservation strategy developed by local stakeholders (KVRI Burbot Committee 2005). Burbot in the Kootenai River have been subject to extensive sampling efforts over the last decade by personnel of the Idaho Department of Fish and Game (IDFG) to assess burbot abundance, distribution, length structure, reproductive success, and movement and to identify factors limiting burbot recruitment (Paragamian 2000; Paragamian et al. 2000, 2005). This information is critical for the development of effective conservation and rehabilitation measures. This paper synthesizes results of this long-term sampling program.

## Study Area

The Kootenai River (spelled Kootenay for Canadian waters) is one of the largest tributaries to the Columbia River (Bonde and Bush 1975). Originating in Kootenay National Park, British Columbia, the river discharges south into Montana, where Libby Dam forms Koocanusa Reservoir and impounds water into Canada (Figure 1). From Libby Dam, the river discharges west and then northwest into Idaho, then north into British Columbia and Kootenay Lake. The Kootenai River at Porthill, Idaho, near the border with British Columbia, drains about 35,490 km<sup>2</sup>. The Kootenai River Reach in Idaho from river kilometer (rkm) 170 to rkm 276 is 106 km long. Kootenay Lake is a large 39,537-ha oligotrophic lake that has two major inlets, the Duncan River to the north and the Kootenai River to the south.

The Idaho reach is characterized by three segments with different channel types: (1) steep canyon walls and a high gradient (~0.6 m/km) typify the corridor from the Montana Border to the Moyie River; (2) for about 13 km downstream of the confluence with the Moyie River to Bonners Ferry, the river follows a braided channel; and (3) downstream of Bonners Ferry, the river meanders through a broad floodplain between the Selkirk and Purcell Mountains with a lower gradient of about 0.02 m/km. Tributary streams are typically high gradient as they pass through mountain canyons, but revert to lower gradients when they reach the Kootenai River floodplain.

## Methods

### *Adult Sampling*

Sampling for burbot was conducted annually from 1993 through 2004 in cooperation with the British Columbia Ministry of Environment (BCME). Adult burbot were captured using baited hoop nets primarily during the

winter to coincide with spawning and post-spawning migrations. Hoop nets had a maximum diameter of 0.61 m (see Bernard et al. 1991 and Paragamian 1995 for a description of the nets and the method of deployment). Catch per unit of effort (CPUE) was measured as one 24-h set for each net, with one net day equaling one unit of effort.

Nets were deployed in deep areas (usually > 8 m or the thalweg) of the Kootenai River between rkm 123 (south arm of Kootenay Lake) and rkm 245.5 (Ambush Rock). Sampling further upriver to rkm 270 (the Montana border) occurred only in 1993 (Figure 1). Although effort was widely distributed, it was concentrated at rkm 170 (Boundary Creek near Porthill, Idaho), rkm 145 (Nick's Island, British Columbia), rkm 152 (the Goat River, near Creston, British Columbia), and Ambush Rock. Captured burbot were measured for total length (TL) and weighed to the nearest gram. From 1994 through 2004, captured burbot were implanted with a passive integrated transponder tag in the left opercular muscle. Sex of some burbot was determined by gentle abdominal massage and examination of sex products. Some post-spawn fish were biopsied to determine sex and reproductive status. More than 60 burbot were implanted with radio or ultrasonic transmitters (Paragamian 2000; Paragamian et al. 2005).

### 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 those captured fish that were tagged and released; (3) within-season recaptured fish are recapture events that occurred within a single sampling season; and (4) among-season recaptured fish are recaptures after one or more seasons. For some analyses, we organized the capture–recapture data into six different spatial seg-

ments defined by river kilometer. Segment 1 was Kootenay Lake; segments 2, 4, and 6 were long segments of the Kootenai River (segment 6 was sampled in the 1993 winter season but little, thereafter, upriver of Bonners Ferry to rkm 270); and segments 3 (Goat River) and 5 (Ambush Rock and vicinity) were key spawning locations.

### Adult Size

Spatial and temporal patterns in body size of captured adults were analyzed using length data. First, mean lengths of captures among river segments were compared using analysis of variance (ANOVA). Data for four key segments (segments 2, 3, 4, and 5) were then pooled across consecutive 3-year periods to examine potential changes in length distributions over time. This level of data aggregation provided adequate sample sizes for comparing distributions. Mean lengths by period were compared using ANOVA, and linear regression was used to assess the temporal trend in annual estimates of mean length.

### Abundance Estimates

Abundance and survival were estimated using variations of the Jolly–Seber model applied to among-season recapture data. The Jolly–Seber model is applicable to open populations subject to mortality (or permanent emigration) and recruitment (or immigration) (Seber 1982:196). 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 ( $p_i$ ) and survival rates ( $\phi_i$ ). In turn, these estimates are used to estimate abundance ( $N_i$ ) and net recruitment ( $B_i$ ) by period. The accuracy and reliability of estimates depends on the number of recaptures and the degree to which assumptions of the model are met. Seber (1982) suggested that at least 10 recaptures per release period and

per recovery period are required to provide reasonable estimates of  $p_t$  and  $\phi_t$ .

However, the total number of among-season recaptures for a given release year or recovery year ranged from zero to a maximum of eight during this Kootenai burbot study. Given so few recaptures, the number of parameters in the model had to be reduced (e.g., Brownie et al. 1986). Two alternative models were explored (Pyper et al. 2004). In the first model (denoted the no-effort model), data were pooled across the four key river segments 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 hoop-net effort ( $E_t$ ; Seber 1982:296):

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

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 ( $\bar{E}_t = E_t / \bar{E}$ ) 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 the effort model.

Six additional models were tested by Pyper et al. (2004) in which river segments were divided into two different groups, and capture probabilities ( $p$ ) and survival rates ( $\phi$ ) were either modeled as identical or dif-

ferent between the two groups (including models with or without sampling effort). These models were examined to account for potential differences in capture–recapture rates within and among the river segments, as well as notable differences in sampling effort across years among the segments. However, these models provided similar results to the combined-segment models described above (Pyper et al. 2004). We therefore limit our presentation of results to the combined-segment models.

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 less than 4, 4–7, or more than 7, respectively (Burnham and Anderson 1998). Unlike the standard Jolly–Seber model, there are no analytical formulas for computing standard errors and confidence intervals for reduced-parameter models (Brownie et al. 1986). We therefore used likelihood theory (Kendall and Stuart 1979; Schnute 1992) to estimate approximate confidence intervals for one selected model. For example, the approximate 95% confidence or likelihood interval for a given parameter is defined by parameter values for which the log-likelihood is 1.92 less than the maximum log-likelihood (integrated across all other parameters). For all models, estimates of annual abundance ( $N_t$ ) and net recruitment ( $R_t$ ) 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., slope[ $N_t$  versus  $t$ ]/ $\bar{N}$  \* 100).

### Population Model

The deterministic model described in this section was used 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 following form of the von Bertalanffy (LVB) growth model (Quinn and Deriso 1999):

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

where  $L$  is the length of fish  $i$  at age  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is a growth coefficient defining curvature, and  $t_0$  is interpreted as the age when an individual would have been at length 0 had the growth model been operative at all ages (Ricker 1975; Quinn and Deriso 1999). Errors ( $w$ ) were assumed to be additive and normally distributed with a mean of zero and standard deviation  $\sigma_w$ .

To establish initial growth parameters for Kootenai burbot, we fit the LVB model to the capture–recapture data. 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

$\Delta t_i$  was the elapsed number of days among periods. In this formulation, only  $L_\infty$  and  $K$  can be estimated via maximum likelihood (nonlinear least squares). 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 intersected the  $x$ -axis (zero length) between hypothetical ages 0 and  $-1$ .

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,  $n_1$  defined the slope of the selectivity curve and  $n_2$  was 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).

## Results

### Summary of Adult Sampling

Across years, there was a total of 403 fish captures, from which 300 burbot were tagged and released (Table 1). Of the remaining 103 fish captures, 45 were within-season recaptures, 27 were among-season recaptures, and 31 were not tagged. Twenty-four of the

TABLE 1. Summary of annual adult burbot captures and recaptures in the Kootenai River, 1993–2004. 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).

Year	Captured			Recaptured												Percent recaptured	
	Total captured	New tags	Among-season recaptures	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004		Total
1993	17	15	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0%
1994	15	9	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%
1996	34	30	0	-	-	-	-	3	3	2	0	0	0	0	0	8	27%
1997	24	21	3	-	-	-	-	-	0	0	0	0	0	0	0	0	0%
1998	59	50	3	-	-	-	-	-	-	1	0	0	0	0	0	1	2%
1999	47	40	3	-	-	-	-	-	-	-	1	1	0	0	0	2	5%
2000	36	31	1	-	-	-	-	-	-	-	-	7	2	0	1	10	32%
2001	74	40	8	-	-	-	-	-	-	-	-	-	5	0	1	6	15%
2002	33	19	7	-	-	-	-	-	-	-	-	-	-	0	0	0	0%
2003	11	10	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0%
2004	20	15	2	-	-	-	-	-	-	-	-	-	-	-	-	0	0%
Total	403	300	27	0	0	0	0	3	3	3	1	8	7	0	2	27	9%

300 marked burbot were captured initially in Kootenay Lake, and 1 was recaptured. None of the burbot tagged in 1993–1995, 1997, or 2003 was recaptured in subsequent years, although there were some within-year recaptures (Table 2). The total number of among-season recaptures for a given release year or recovery year ranged from zero to a maximum of eight.

Hoop-net effort varied annually, but generally increased over time and ranged from 554 net days in 1993 to 2,085 in 2001 (Figure 2). Catch also increased until 2001, then declined substantially (Figure 2). Catch per unit of effort varied from 1993 through 1998 (range = 0.029–0.054 burbot/net day) and declined steadily thereafter (Figure 2). Although the majority of captures occurred in river segments 3 and 5, more effort was devoted across years to segments 2 and 4 (Table 2).

### Adult Length

The length–frequency distribution for all captured burbot was bell shaped and highly symmetric, ranging from 300 to 958 mm TL, with mean = 578 mm (SD = 117 mm). There were obvious spatial and temporal differences in lengths of captured fish. Across all years, length distributions were remarkably consistent for segments 2 through 5, but fish cap-

tured in segment 1 (Kootenay Lake) tended to be much larger. Mean lengths for segments 2–5 were similar (560, 565, 577 and 569 mm TL, respectively) while mean length for segment 1 (743 mm TL) was significantly larger (ANOVA,  $P < 0.001$ ).

Consequently, to analyze temporal trends in length, we omitted fish from segment 1 because of their anomalous mean length and because most fish were captured in only 2 years (1996 and 1998). For the remaining data (pooled across segments 2–5), there was a clear trend toward larger lengths over time (Figure 3). Length distributions for combined 3-year periods showed subtle but important differences. For the first 3-year 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. Differences in mean lengths for the four periods were highly significant (ANOVA,  $P < 0.001$ ; Figure 3). Across year, mean length increased by roughly 8 mm/year on average from 1993 (516 mm) to 2004 (629 mm).

### Abundance Estimates

Seber-Jolly abundance and survival estimates were first calculated using data pooled across river segments 2–5 for sampling seasons 1996–2004. As noted earlier, none of

TABLE 2. Kootenai River burbot capture data (across all gear types) by segment, 1993–2004 (IDFG winter hoopnet effort only, a 24-h set is one unit of effort).

Segment	rkm	Description	Hoopnet effort (net day)	Captures	Tagged	Recaptures	
						Within-season	Among-season
1	15.7–121.9	Kootenay Lake	not available	24	16	1	0
2	123.5–152.6	Kootenai River	3,628	76	65	1	5
3	152.7	Goat River	1,560	127	103	8	7
4	153.6–242.0	Kootenai River	7,238	46	39	3	2
5	244.2–245.0	Ambush Rock	2,896	129	76	32	13
6	249.4–270.0	Kootenai River	186	1	1	0	0
Totals				403	300	45	27

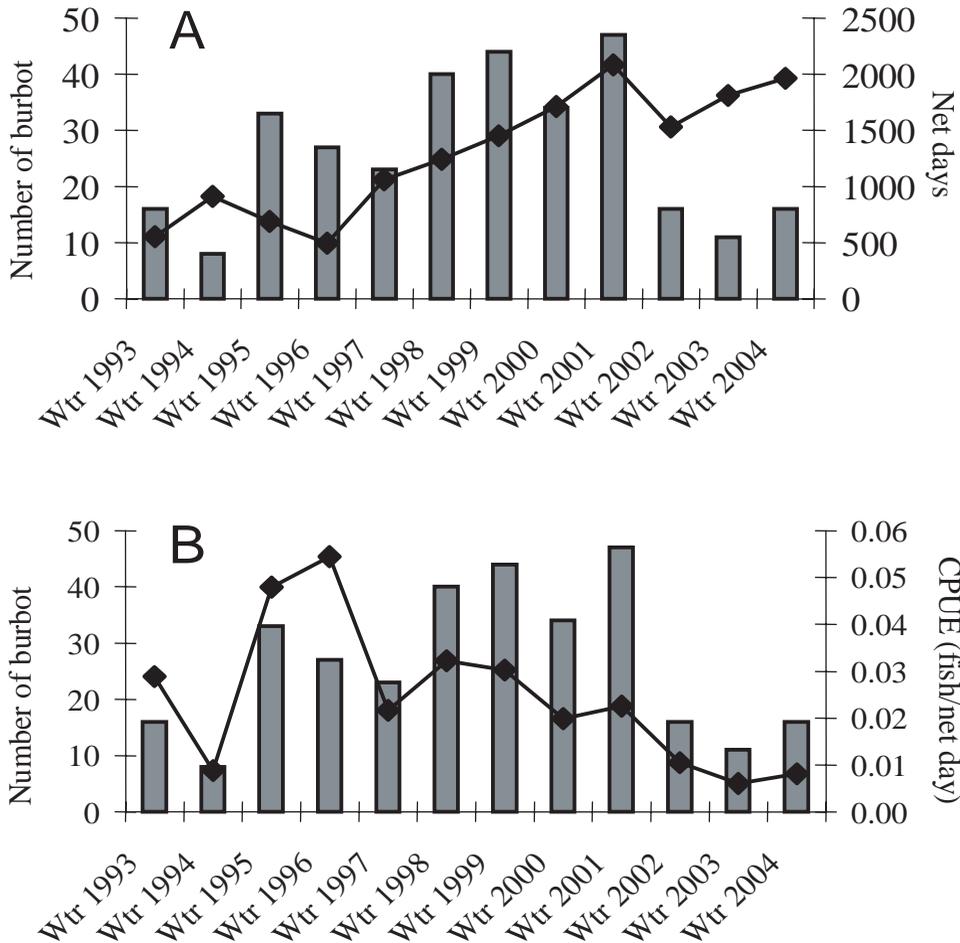


FIGURE 2. (A) Kootenai River burbot catch (bars) and sampling effort (line) from 1993 to 2004 (IDFG winter hoopnet effort only). (B) Kootenai River burbot catch (bars) and CPUE (line) from 1993 to 2004 (IDFG winter hoop-net effort only).

the burbot tagged in the 1993–1995 seasons were recaptured during subsequent seasons, and hence, these years were omitted from analyses. The models assumed that all living fish had equal probabilities of capture across segments. The effort model for the combined segment provided a slightly better fit (lower AIC) than the no-effort model, but both models provided similar parameter estimates (Table 3). 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 3). Abundance estimates for both models declined over time (Figure 4), though the average decline was greater for the effort model (14%/year) than for the no-effort model (8%/year). Larger declines were evident for recruitment estimates (Figure 4). In this case, the decline was greatest for the no-effort model (Table 3).

The precision of parameter estimates and implications for abundance estimates

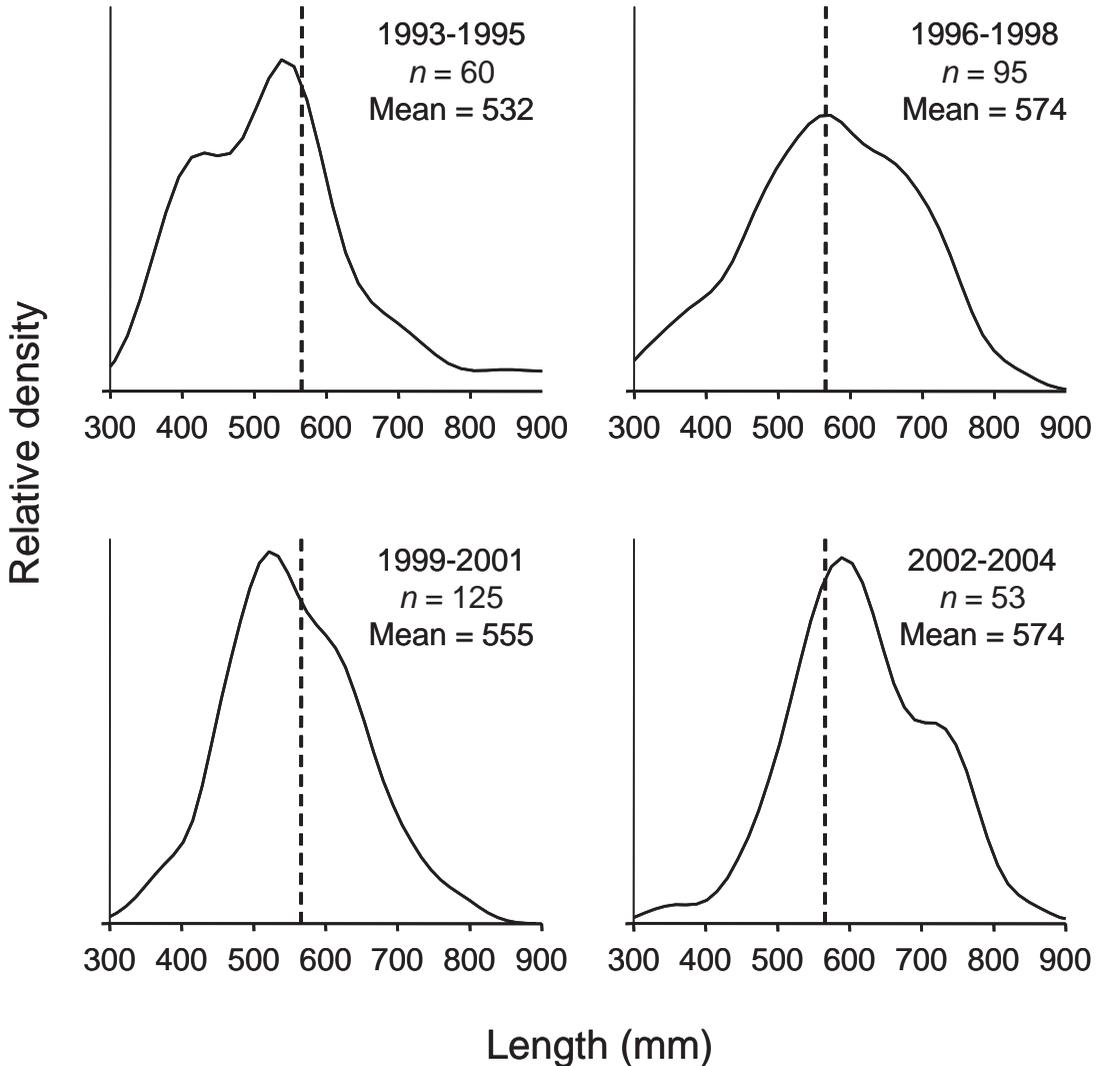


FIGURE 3. Length distributions for burbot captured in river segments 2–5 (dashed line is the grand mean).

were explored for the effort model. The 95% confidence intervals for each parameter indicated considerable uncertainty (Table 3). Abundance estimates, however, were far more sensitive to changes in  $\hat{p}$  than  $\hat{\phi}$ . The approximate 95% confidence interval for  $\hat{p}$  corresponded to a range of  $\hat{N}$  from 85 at  $\hat{p} = 0.41$  and 294 at  $\hat{p} = 0.12$  (Figure 5). Changes to either  $\hat{p}$  or  $\hat{\phi}$  essentially scaled all annual abundance estimates either upward or

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

#### Population Model

Initial parameters used in the population model were based on empirical estimates from the capture–recapture models and estimated growth curve. Specifically, LVB growth parameters were set at  $K = 0.05$ ,  $L_{\infty}$

TABLE 3. Parameter and abundance estimates for capture-recapture models (segments 2–5). Approximate 95% confidence intervals for parameters of the “effort” model are shown in parentheses.  $p$  = capture probability;  $\phi$  = survival rate;  $N_t$  = annual abundance;  $B_t$  = annual recruitment.

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

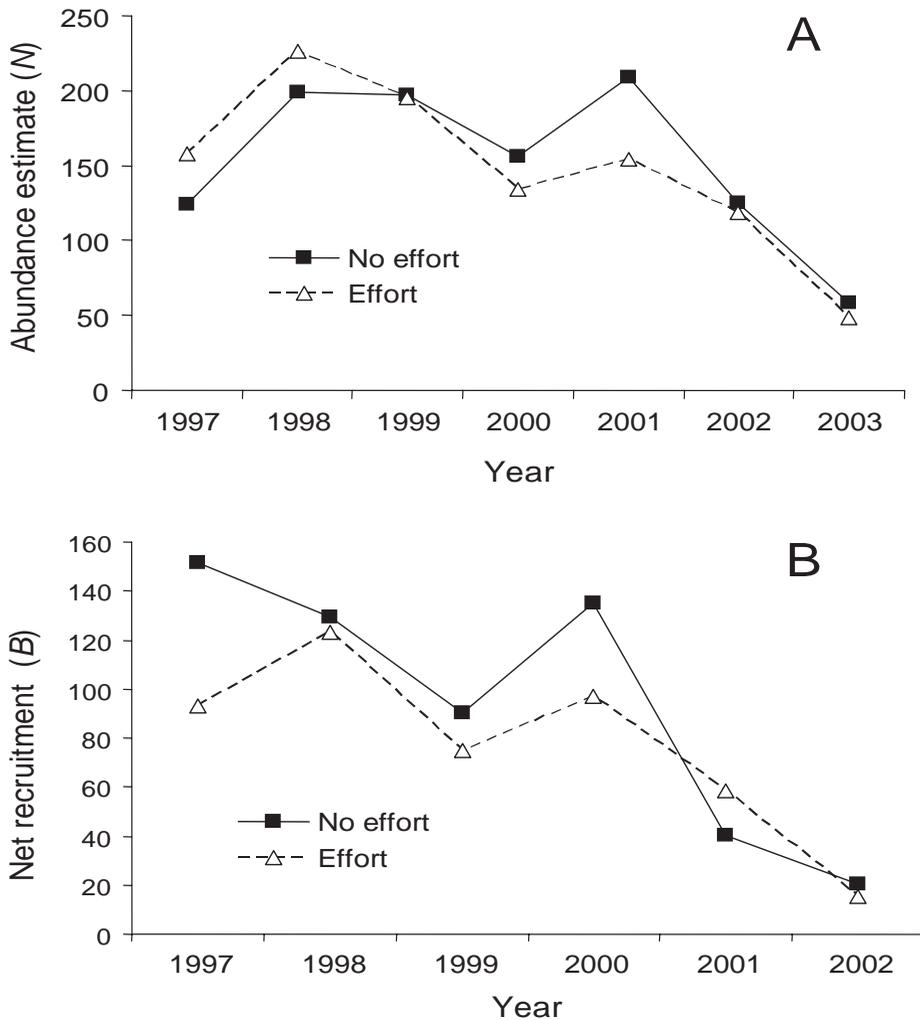


FIGURE 4. (A) Estimates of Kootenai River burbot abundance ( $N_t$ ) for capture-recapture models (river segments 2–5). (B) Estimates of Kootenai River burbot recruitment ( $B_t$ ) for capture-recapture models (segments 2–5). The effort model accounted for annual variation in total hoop-net effort across segments 2–5 when estimating the capture probability ( $p$ ).

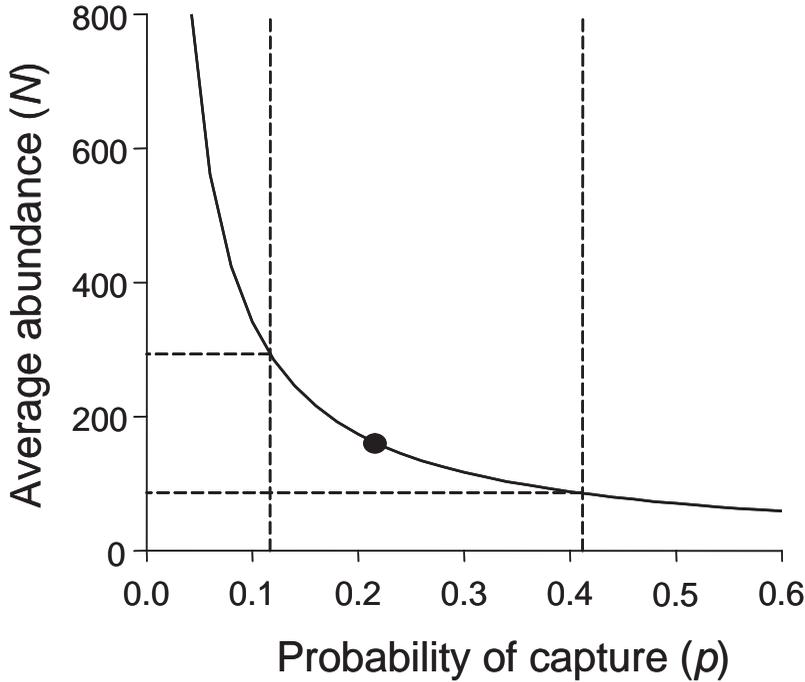


FIGURE 5. Estimates of average Kootenai River burbot abundance (river segments 2–5, 1997–2003) as a function of capture probability ( $p$ ) for the effort model. Horizontal lines indicate the 95% confidence interval for  $p$  and the corresponding average abundances (integrated across  $\phi$ ).

$= 1,500$ ,  $t_0 = -1$ , and  $\sigma_w = 0.5$  (Figure 6). 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 from segments 2–5 (mean = 566 mm and SD = 108 mm).

The expected length–frequency given the initial parameter values was skewed strongly toward shorter lengths than those of the observed length distribution (Figure 7). Under constant recruitment, more young fish will be in this population. Thus, to approximate the symmetry of the observed distribution, relative capture vulnerabilities of younger fish had to be reduced. However, it is also evident that few fish were expected to obtain lengths greater than 500 mm (Figure 7). In fact, we found no reasonable selectivity curve to reproduce

the observed length distribution given the initial growth and survival parameters.

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 4). First, we increased the survival rate ( $\phi$ ) to 0.6, a value greater than the upper 99% confidence interval for the effort model. Estimates of selectivity parameters were roughly  $n_1 = 1.3$  and  $n_2 = 7.4$  (5, case 1), providing a reasonable approximation of the observed length distribution (Figure 7). However, this implied a slow increase in selectivity with fish at about age 7 (mean length = 529 mm) having a 50% capture vulnerability. Across ages 3–12, the vulnerable proportion of the population was only 17% (Table 4, case 1).

In the second scenario, LVB parameters were changed to  $K = 0.18$ ,  $L_\infty$  (with  $\phi$  set back

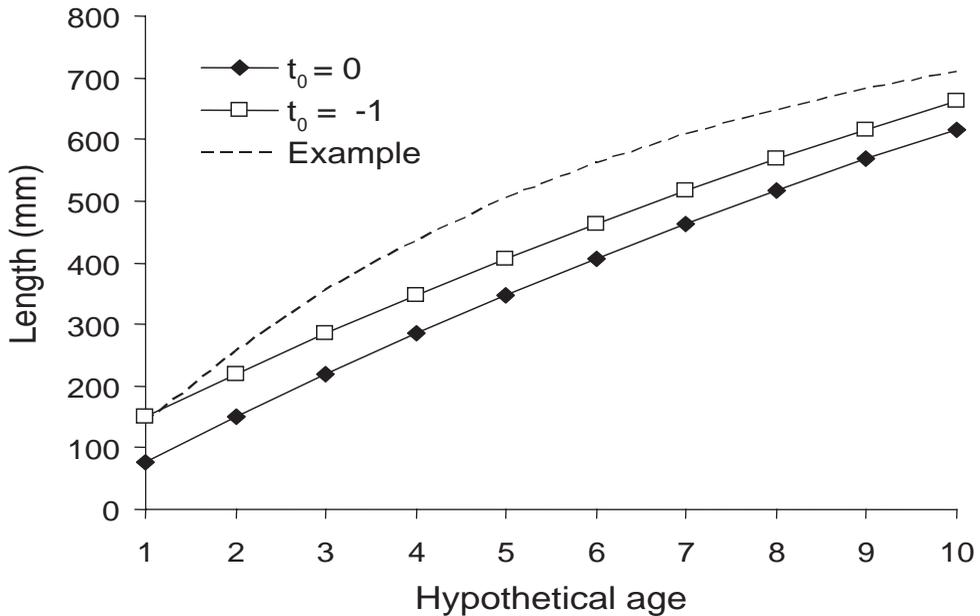


FIGURE 6. Length-age curves based on the length von Bertalanffy model fit to recapture data for Kootenai River burbot ( $K = 0.05, L_{\infty} = 1,500$ ). Curves are shown for two assumed values of  $t_0$  (0 and -1) and a hypothetical example ( $K = 0.18, L_{\infty} = 850$ , and  $t_0 = 0$ ).

to 0.4). These parameters imply more rapid growth and provide a growth curve (Figure 6) that is very similar to that presented in Katzman and Zale (2000) for burbot from Lake of the Woods, Ontario, in the mid-range of burbot populations. Again, however, the corresponding estimates for  $n_1$  and  $n_2$  implied very low capture vulnerabilities across ages (Table 4, case 2).

The third scenario included both increased survival and growth rates, which yielded a more reasonable selectivity curve (Table 4, 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 was to mimic the observed increase in mean length over time via a simple exponential decline in recruitment. Again, high survival and growth rates were assumed, as well as a steep-

er selectivity curve (Table 4, 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 8). 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 four 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.

## Discussion

Several assumptions underlie the abundance and recruitment estimates of our burbot models (e.g., Seber 1982): (1) every fish, whether

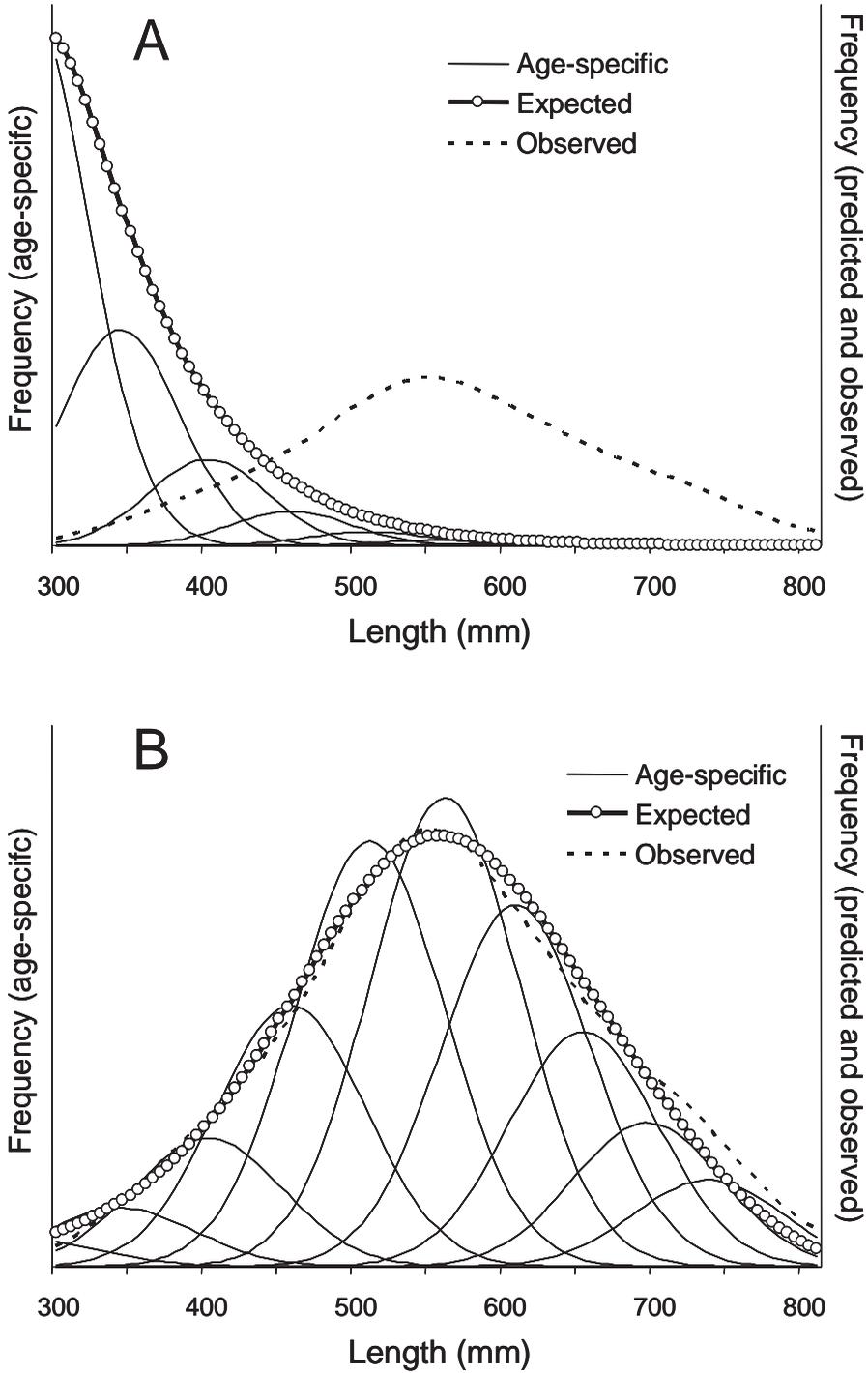


Figure 7. (A) Length–frequency distributions (relative densities) for initial parameter values of the population model (ages 3–12) of Kootenai River burbot. (B) Length–frequency distributions given parameter values for case 1 (see Table 4). The expected distribution integrates across age-specific distributions.

TABLE 4. Parameter values for different scenarios of the population model. Also shown are mean lengths at age  $n_2$  (age of 50% vulnerability to fishing gear) and the vulnerable proportion of the population (ages 3–12). The vulnerable proportions for Case 4 correspond to values in year 1 and year 10, respectively. See text for details.

Case	$K$	$L_\infty$	$t_0$	$\phi$	$n_1$	$n_2$	Length at $n_2$	Proportion vulnerable
1	0.05	1,500	-1	0.6	1.3	7.4	529	17
2	0.18	850	0	0.4	1.5	6.0	561	18
3	0.18	850	0	0.6	1.5	5.0	507	51
4	0.18	850	0	0.6	2.5	4.0	436	78, 89

tagged or untagged, has the same probability of capture either across all sampling seasons (no-effort model) or within a given sampling season (effort model); (2) every tagged fish has the same probability of surviving from one period to the next and of being present in the population during subsequent sam-

pling 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, we assumed

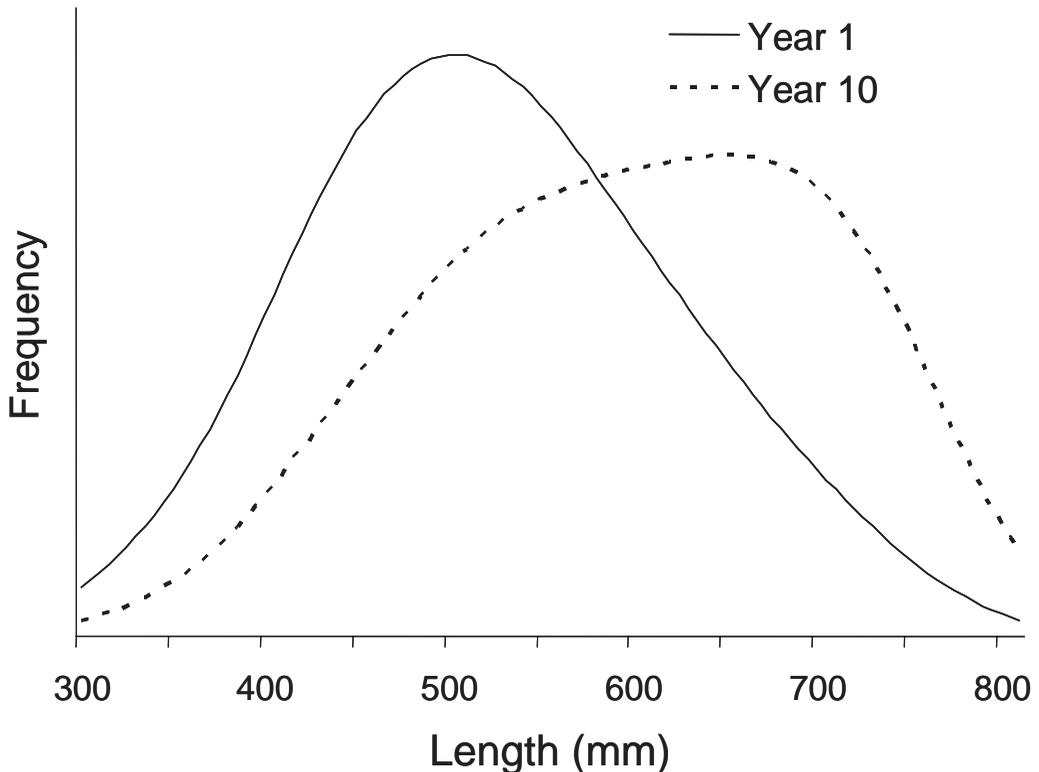


FIGURE 8. Expected length–frequency distributions for Kootenai River burbot in years 1 and 10 given an annual decline in recruitment of 30% with parameter values for case 4 in Table 4.

that capture probabilities were equal across segments, equal 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 segment and seasons. Assumption 2 may be valid; the Jolly–Seber model allows for permanent emigration, but not temporary emigration. We believe burbot attempted to migrate to spawn most years. Telemetry records indicated all burbot tagged with transmitters were within the sampling area each year (Paragamian 2000; Paragamian et al. 2005). Assumption 3 was likely satisfied. With respect to assumption 4, we used only among-season recaptures such that survival rates pertained to a period (roughly 1 year) greater than the sampling period. Across assumptions, violations of assumption 1 were likely the most serious. Nevertheless, results were generally consistent across models with or without effort data, including the six additional models explored by Pypker et al. (2004) in which river segments were separated into two groups. 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.

We expect that burbot in the Kootenai River will reach extinction within the next 10 years unless effective immediate remedial measures are taken. Analyses of 12 years of capture–recapture data indicated that the burbot population has declined, recruitment has been insufficient, and the population is probably 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 length. Yet, in 2000, Kootenai River burbot were petitioned for listing as threatened under the U.S. Endangered Species Act, but the U.S. Fish and Wildlife

Service found in 2003 that listing was not warranted because the fish did not represent a distinct population segment (U.S. Federal Register 2003).

Estimates of adult burbot abundance ranged from 225 for 1997 to 50 fish in 2003, depending on the model. Although these estimates were based on few recaptures and simplified assumptions, they seem reasonable. For example, 12 years of sampling produced only 403 captures, of which 72 were recaptures. In recent years, we collected fewer than 15 captures annually despite high sampling effort (Paragamian et al. 2004). Of course, abundance estimates pertain only to the vulnerable portion of the burbot population in a portion of the study area. For this reason, population estimates are likely conservative and apply to the age- and length-groups vulnerable to our gear. Partridge (1983) aged burbot in the Kootenai River using otoliths and found that age-1 and age-2 fish were about 200 and 340 mm TL, respectively. Based on studies by Bernard et al. (1991), burbot can be caught in hoop nets at about 350 mm TL but are not fully recruited until 450 mm TL.

Catch rates for Kootenai River burbot are near the low end of values reported in other areas. Kootenai River CPUE ranged from 0.054 in 1996 to a low of 0.008 in 2004. Although gear types differed (hoop nets versus cod traps; Spence 2000), the Kootenay Lake Balfour fishery CPUE was between 0.02 and 0.06 (Redfish Consulting, Ltd. 1998). By comparison, CPUE in the Tanana and Chena rivers, Alaska, with hoop nets was greater than 1.0 and 0.5, respectively (Evenson 1993). Catch per unit effort of burbot in four Alaskan Lakes ranged from 0.5 to 3.0 (Parker et al. 1988).

Although annual hoop-net effort was distributed throughout the river, consistent capture of burbot occurred in only two locations: Ambush Rock, Idaho and in or near the Goat River, British Columbia. These two locations

likely represent spawning locations. During the winter of 2000–2001, we captured more than 20 burbot at Ambush Rock, and both male and female burbot were identified as gravid, discharging, 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, 1995, 2000; Paragamian and Whitman 1996, 1997, 1998; Kozfkay and Paragamian 2002). We have no evidence of burbot spawning in other areas of the Kootenai River from Kootenay Lake upstream to the Idaho–Montana border. However, no burbot were captured in the Goat River from 2002 through 2005, suggesting that this stock may be extinct (Paragamian and Laude 2006). Analysis of the capture and recapture locations suggested considerable site fidelity among Kootenai River burbot (Pyper et al. 2004). In many cases, burbot were captured at the same location over multiple years, particularly in the Goat River and Ambush Rock areas (Kozfkay and Paragamian 2002; Paragamian and Laude 2006).

Although burbot spawning and recruitment was documented, observed declines in adult abundance and the general lack of small burbot (e.g., <500 mm) in recent years indicated that recruitment rates were too low to sustain a significant population. Our burbot population model suggested that 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 due to low numbers of adults are unknown. But the capture and recaptures of unspent adults following the spawning season suggested many burbot were not spawning (Paragamian 2000; Paragamian et al. 2001).

Length–frequency distributions of cap-

tures suggest reasonable growth by adult burbot in the Kootenai River over the period 1993–2004. The length distribution of burbot across 1993–2004 was similar to that of burbot harvested in the Balfour fishery in Kootenay Lake from 1968 to 1975 (Redfish Consulting, Ltd. 1998). Although the most common length of Kootenai River burbot was between 500 and 600 mm, compared to 650–750 mm for the Balfour fishery, there was still a substantial proportion of burbot greater than 700 mm 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 500–600 mm were dominated by ages 5–7. Lower growth rates would necessitate higher survival rates and would result in older fish in these length-classes.

In contrast, estimates of survival rate were unreasonably low for the unexploited Kootenai River burbot population. Capture–recapture estimates of an annual survival rate of roughly 40% (i.e., 60% annual mortality) were not consistent with observed length distributions and anticipated growth rates, which implied that much lower mortality rates (e.g., 40%) were required to achieve the observed length distributions. Such discrepancies may be due to sampling error in the capture–recapture data or may reflect adverse effects of capture, handling, and tagging on adult burbot (Neufeld and Spence 2005). By comparison, the estimated annual mortality rate of burbot in the Kootenai River was similar to the heavily exploited Lake of the Woods 64% (Muth and Smith 1974) but at the high end for published studies of other burbot populations: southwestern Lake Superior 39% (Bailey 1972), Lake Erie 40% (Clemens 1951), Lake Erie from 1994 to 2003 at 33% (Stapan-

ian and Madenjian 2007), and western Lake Superior 43% (Schram 2000).

Collectively, our results indicate that the Kootenai River burbot population is rapidly approaching or has already reached functional extinction. Theoretical conservation biologist and geneticists estimate that a minimum effective breeding population ( $N_e$ ) of at least 50–500 individuals is necessary to sustain a viable population (Soule 1980; Lande and Barrowclough 1987). Genetic and demographic risks and uncertainties of smaller numbers are high (Musick 1999; McElhany et al. 2000; Allendorf and Ryman 2002). 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 and loss of stocks that spawn in specific locations. Yet, burbot have shown resilience to rehabilitation or recovery efforts when fishing or environmental issues are resolved (Bruesewitz 1990; Taube 2000; Stapanian et al. 2008, this volume).

The acute status of the Kootenai River burbot population presents some difficult choices for conservation and recovery efforts. Current voluntary efforts to maintain low winter discharges, thought to be conducive for burbot migration and spawning, have been insufficient to arrest population declines or to restore significant burbot recruitment (Paragamian et al. 2005). Discharge measures at Libby Dam have been shown to impair spawning migration of burbot (Paragamian 2000; Paragamian et al. 2005) and water temperature changes may have affected migration timing (Paragamian and Wakkinen 2008, this volume), but it is not fully understood how other ecosystem changes such as, diking, flood plain disconnection, channelization of tributary streams, nutrient losses, or biological changes in the system may have

also negatively affected burbot life histories. Suitable habitat conditions must be immediately restored to improve prospects of recovery of the small remnant population. 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 nonnative stocks may not do well and could speed extinction of the locally adapted native population.

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### References

- Allendorf, F. W., and N. Ryman. 2002. The role of genetics in population viability analysis. Pages 50–85 in S. A. Beissinger and D. R. McCullough, editors. Population viability analysis. The University of Chicago Press, Chicago.
- Anders, P. J., D. L. Richards, and M. S. Powell. 2002. The first endangered white sturgeon population: repercussions in an altered large river-floodplain ecosystem. Pages 67–82 in W. Van Winkle, P. J. Anders, D. H. Secor, and

- D. A. Dixon, editors. Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, Maryland.
- Argent, D. G., R. F. Carline, and J. R. Stauffer, Jr. 2000. A method to identify and conserve rare fishes in Pennsylvania. *Journal of the Pennsylvania Academy of Science* 74:3–12.
- Arndt, S., and J. Hutchinson. 2000. Characteristics of a tributary-spawning population of burbot from Columbia Lake. Pages 48–60 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Bailey, M. M. 1972. Age, growth, reproduction of the burbot, in southwester Lake Superior. *Transactions of the American Fisheries Society* 101:667–674.
- Bernard, D. R., G. A. Pearse, and R. H. Conrad. 1991. Hoop traps as a means to capture burbot. *North American Journal of Fisheries Management* 11:91–104.
- Bonde, T. H., and R. M. Bush. 1975. Kootenai River water quality investigations, Libby Dam pre-impoundment study 1967–1972. U.S. Army Corps of Engineers, Washington, D.C.
- Brownie, C., J. E. Hines, and J. D. Nichols. 1986. Constant parameter capture-recapture models. *Biometrics* 42:561–574.
- Bruesewitz, R. E. 1990. Population dynamics and movement of burbot (*Lota lota*) in western Lake Michigan and Green Bay. Master's thesis. University of Wisconsin, Stevens Point.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Clemens, H. P. 1951. The growth of burbot in Lake Erie. *Transactions of the American Fisheries Society* 80:163–173.
- Edsall, T. A., G. W. Kennedy, and W. H. Horns. 1993. Distribution, abundance, and resting microhabitat of burbot on Julian's Reef, southwestern Lake Michigan. *Transactions of the American Fisheries Society* 122:560–574.
- Evenson, M. J., and P. Hansen. 1991. Assessment of harvest characteristics of the Tanana River burbot sport fishery in 1990 using a postal questionnaire. Alaska Department of Fish and Game, Fisheries Data Series Number 91–67, Anchorage.
- Evenson, M. J. 1993. A summary of abundance, catch per unit of effort, and mean length estimates of burbot sampled in rivers of interior Alaska. Alaska Department of Fish and Game, Fishery Data Series Number 93–15, Anchorage.
- Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Katzman, L. M., and A.V. Zale. 2000. Age and growth of an unexploited burbot population in upper Red Rock Lake, Montana. Pages 139–146 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Keith, P., and Allardi, J. 1996. Endangered freshwater fish: the situation in France. Pages 35–54 in A. Kirchover and D. Hefti, editors. *Conservation of endangered freshwater fish in Europe*. Birkhäuser Verlag, Basel, Switzerland.
- Kendall, M., and A. Stuart. 1979. The advanced theory of statistics. Volume 2: inference and relationship. 4th edition. MacMillan, New York.
- Kozfkay, J. R., and V. L. Paragamian. 2002. Kootenai River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Annual Progress Report, Project 88–65, Boise.
- KVRI (Kootenai Valley Resource Initiative) Burbot Committee. 2005. Kootenai River/Kootenay Lake burbot conservation strategy. Prepared by the Kootenai Tribe of Idaho with assistance from S. P. Cramer and Associates, Bonners Ferry.
- Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–123 in M. E. Soule, editor. *Viable populations for conservation*. Cambridge University, New York.
- Maitland, P. S., and A. A. Lyle. 1990. Practical conservation of British fishes: current action

- on six declining species. *Journal of Fish Biology* 37(Supplement A):255–256.
- Maitland, P. S., and A. A. Lyle. 1996. Threatened freshwater fishes of Great Britain. Pages 9–21 in A. Kirchover and D. Hefti, editors. *Conservation of endangered freshwater fish in Europe*. Birkhäuser Verlag, Basel, Switzerland.
- McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42, Seattle.
- McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. *Fisheries Research Board of Canada Bulletin* 173.
- Musick, J. A. 1999. Criteria to define extinction risk in marine fishes. *Fisheries* 24:6–14.
- Muth, K., and L. Smith. 1974. The burbot fishery of Lake of the Woods. University of Minnesota, Agricultural Station, Technical Bulletin 290, Minneapolis.
- Neufeld, M., and C. Spence. 2005. Evaluation of a simple decompression procedure to reduce decompression trauma in trap caught burbot. *Transactions of the American Fisheries Society* 133:1260–1263.
- Paragamian, V. L. 1994a. Kootenai River fisheries investigation: stock status of burbot and rainbow trout and fisheries inventory. Idaho Department of Fish and Game. Bonneville Power Administration, Annual Progress Report (1993), Project 88–65, Boise.
- Paragamian, V. L. 1994b. Kootenai River fisheries investigation: stock status of burbot and rainbow trout and fisheries inventory. Idaho Department of Fish and Game. Bonneville Power Administration, Annual Progress Report (1994), Project 88–65, Boise.
- Paragamian, V. L. 1995. Kootenai River fisheries investigation: stock status of burbot and rainbow trout and fisheries inventory. Idaho Department of Fish and Game. Bonneville Power Administration, Annual Progress Report, Project 88–65, Boise.
- Paragamian, V. L. 2000. The effects of variable discharges on burbot spawning migrations in the Kootenai River, Idaho, USA, and British Columbia, Canada. Pages 111–123 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Paragamian, V. L., M. Powell, and J. Faler. 1999. Mitochondrial DNA analysis of burbot in the Kootenai River basin of British Columbia, Montana, and Idaho. *Transactions of the American Fisheries Society* 128:854–86.
- Paragamian, V. L., and Whitman, V. 1996. Kootenai River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Annual Progress Report, Project 88–65, Boise.
- Paragamian, V. L., and Whitman, V. 1997. Kootenai River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Annual Progress Report, Project 88–65, Boise.
- Paragamian, V. L., and Whitman, V. 1998. Kootenai River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Annual Progress Report, Project 88–65, Boise.
- Paragamian, V. L., and D. W. Willis. 2000. Introduction. Page 7 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Paragamian, V. L., V. Whitman, J. Hammond, and H. Andrusak. 2000. Collapse of the burbot fisheries in Kootenay Lake, British Columbia Canada, and the Kootenai River, Idaho, USA, post-Libby Dam. Pages 155–164 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Paragamian, V. L., J. R. Kozfkay, and Whitman, V. 2001. Kootenai River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Annual Progress Report, Project 88–65, Boise.
- Paragamian, V. L., R. Hardy, and B. Gunderman. 2005. Effects of regulated discharge on burbot migration. *Journal of Fish Biology* 66:1199–1213.
- Paragamian, V. L., and C. Laude. 2006. Kootenai

- River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Bonneville Power Administration Annual Progress Report, Project 88–65, Boise.
- Paragamian, V. L., and V. D. Wakkinen. 2008. Seasonal movement of burbot in relation to temperature and discharge in the Kootenai River, Idaho, USA and British Columbia, Canada. Pages 55–77 in V. L. Paragamian and D. Bennett, editors. *Burbot: ecology, management, and culture*. American Fisheries Society, Symposium 59, Bethesda, Maryland.
- Paragamian, V. L., Pyper, B. J., M. J. Daigneault, R. P. Beamesderfer, and S. C. Ireland. 2004. Kootenai River fisheries investigation: burbot stock status. Idaho Department of Fish and Game, Bonneville Power Administration Annual Progress Report, Project 88–65, Boise.
- Parker, J. F., R. Lafferty, W. D. Potterville, and D. R. Bernard. 1988. Stock assessment and biological characteristics of burbot in lakes of interior Alaska during 1988. Alaska Department of Fish and Game, Fishery Data Series 98, Juneau.
- Partridge, F. 1983. Kootenai River fisheries investigations. Idaho Department of Fish and Game, Job Completion Report, Project F-73-R-5, Boise.
- Powell, M., V. L. Paragamian, and J. Dunnigan. 2008. Mitochondrial variation in western North American burbot with special reference to the Kootenai River in Idaho and Montana. Pages 3–27 in V. L. Paragamian and D. Bennett, editors. *Burbot: ecology, management, and culture*. American Fisheries Society, Symposium 59, Bethesda, Maryland.
- Pyper, B. J., M. J. Daigneault, R. P. Beamesderfer, V. L. Paragamian, and S. C. Ireland. 2004. Status and population dynamics of burbot in the Kootenai River, Idaho and British Columbia, Canada. Chapter 2 in V. L. Paragamian, B. J. Pyper, M. J. Daigneault, R. P. Beamesderfer, and S. C. Ireland. *Kootenai River fisheries investigation: burbot stock status*. Idaho Department of Fish and Game, Bonneville Power Administration Annual Progress Report, Project 88–65, Boise.
- Quinn, T. J., II, and R. B. Deriso. 1999. *Quantitative fish dynamics*. Oxford University, New York.
- Quinn, S. 2000. The status of recreational fisheries for burbot in the United States. Pages 127–135 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Redfish Consulting, Ltd. 1998. Investigation of burbot in Kootenay Lake, 1997. Prepared for British Columbia Ministry of Environment, Lands, and Parks, Nelson.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Schnute, J. T. 1992. Statistical analysis of embedded replicates in mark–recovery experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 49:432–442.
- Schram, S. T. 2000. Seasonal movement and mortality estimates of burbot in Wisconsin waters of western Lake Superior. Pages 81–89 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. 2nd edition. Macmillan, New York.
- Soule, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151–170 in M. E. Soule and B. A. Wilcox, editors. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Spence, C. 2000. A comparison of catch success between two styles of burbot traps in lakes. Pages 165–170 in V. L. Paragamian and D. W. Willis, editors. *Burbot biology, ecology, and management*. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.
- Stapanian, M. A., and C. P. Madenjian. 2007. Evidence that lake trout served as a buffer against sea lamprey predation on burbot in Lake Erie. *North American Journal of Fisheries Management* 27:238–245.
- Stapanian, M. A., C. P. Madenjian, C. R. Bronte, M. P. Ebner, B. F. Lantry, and J. D. Stockwell. 2008. Status of burbot populations in the Lau-

- rentian Great Lakes. Pages 111–130 in V. L. Paragamian and D. Bennett, editors. Burbot: ecology, management, and culture. American Fisheries Society, Symposium 59, Bethesda, Maryland.
- Taube, T. T. 2000. Area management report for the recreational fisheries of the upper Copper/upper Susitna River management area, 1996–1997. Alaska Department of Fish and Game, Fishery Management Report 00-4, Anchorage.
- U.S. Federal Register. 2003. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the lower Kootenai River burbot (*Lota lota*) as threatened or endangered. Federal Register 68:47(11 March, 2003):11574–11579.