

The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population

Fiona D. Johnston, John R. Post, Craig J. Mushens, Jim D. Stelfox, Andrew J. Paul, and Brian Lajeunesse

Abstract: An exploited bull trout, *Salvelinus confluentus*, population experienced a 28-fold increase in adult density during a 10-year period from a minimum of 60 individuals. This demonstrates the extent to which this population was overharvested. Its ability to respond in fewer than two generations to the implementation of zero-harvest regulations suggests this population was growth-overfished not recruitment-overfished. Examination of stock–recruitment relationships of various life stages indicates that recovery of this population was regulated by the density-dependent survival of juveniles in the rearing creek. This compensatory response occurred between egg deposition and age-1 and regulated the number of fish recruiting into the adult population. A second population bottleneck became apparent later in the recovery process when density-dependent survival of the adult population resulted in its approach to an asymptote, highlighting the necessity of long-term data sets for examining these compensatory responses. Results from this study demonstrate the importance of understanding the influence of individual life stages on the ability of overexploited populations such as threatened bull trout to recover and for their future management.

Résumé : Une population exploitée d'ombles à tête plate, *Salvelinus confluentus*, a connu une augmentation de densité de l'ordre de 28 fois des adultes durant une période de 10 ans à partir d'un minimum de 60 individus. Cela démontre le degré de surexploitation de la population. Sa capacité de réagir en moins de deux générations à la mise en application d'un règlement d'interdiction absolue des récoltes laisse croire que la population était surexploitée quant à la croissance, mais non quant au recrutement. L'examen des relations stock–recrutement des divers stades du cycle biologique indique que la récupération de cette espèce est contrôlée par la survie dépendante de la densité des jeunes dans le cours d'eau d'élevage. Cette réaction compensatoire se produit entre la ponte des oeufs et l'âge 1 et contrôle le nombre de poissons qui entrent dans la population adulte. Il se produit un second goulot d'étranglement plus tard dans le processus de récupération lorsque la survie dépendante de la densité de la population adulte a pour effet de lui faire atteindre une asymptote; cela illustre la nécessité d'obtenir des séries de données à long terme pour étudier ce type de réponse compensatoire. Les résultats de notre étude démontrent l'importance de comprendre l'influence des divers stades du cycle sur la capacité de récupération d'une population surexploitée, telle que celle de l'omble à tête plate, une espèce menacée; ils sont aussi importants pour sa gestion future.

[Traduit par la Rédaction]

Introduction

By the end of the 20th century, many marine and freshwater fish populations were severely overharvested (Pauly et al. 2002; Post et al. 2002; Hilborn et al. 2003). This leads us to question whether these populations will be able to recover from their depressed levels of abundance and what factors will influence their recovery. Theory suggests that the reduction in competition and cannibalism at low densities allows populations to recover from low levels through compensatory density dependence, where increased juvenile survival

compensates for decreased egg production (Frank and Brickman 2000; Walters and Kitchell 2001; Milner et al. 2003). However, at these low population densities, density-dependent processes or Allee effects, which result in decreased survival or further reduced fecundity at low densities, may result in population collapse even after harvest mortality is removed (Frank and Brickman 2000; Walters and Kitchell 2001). Abiotic factors also affect population abundance (Armstrong et al. 2003; Milner et al. 2003). Fisheries biologists need to understand the influence of compensatory, density-dependent, and density-independent processes on

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F.D. Johnston,¹ J.R. Post, C.J. Mushens, and A.J. Paul. Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada.

J.D. Stelfox. Alberta Sustainable Resource Development, 2nd Floor Provincial Building, 213 – 1 Street West, Cochrane, AB T4C 1B4, Canada.

B. Lajeunesse. Alberta Sustainable Resource Development, 2nd Floor Provincial Building, 800 Railway Avenue, Canmore, AB T1W 1P1, Canada.

¹Corresponding author (e-mail: fdjohnst@ucalgary.ca).

Fig. 1. Lower Kananaskis Lake and Smith-Dorrien Creek study area in the East Slopes of the Rocky Mountains in southwestern Alberta, Canada. The location of the fish counting fence and traps in 1991 and in all other years is indicated. The sections of the creek where redds were counted are shown with roman numerals.

population abundance to predict the ability of populations to recover and to manage them appropriately in the future.

The degree to which density-dependent and density-independent processes contribute to the regulation of populations not dominated by harvest has long been debated (Sinclair 1989; Berryman et al. 2002; Milner et al. 2003). Some studies that dismiss density dependence as a regulating process may have done so because they were too short in duration or incorporated an insufficient range in density to detect it (Begon et al. 1996; Shea and Mangel 2001; Milner et al. 2003). In addition, for species that have complex life histories and numerous life stages, density dependence may only act upon one life stage for a short period of time (Milner et al. 2003). However, during periods prior to and after this stage, the population is influenced by density-independent processes (Elliott 1994; Jonsson et al. 1998; Milner et al. 2003). If studies do not incorporate the appropriate life stage or period of development, conclusions about the influence of density dependence may differ (Prout and McChesney 1985; Whalen et al. 2000). In general, density-dependent regulation in taxa such as fish and insects with high reproductive rates occurs primarily in the early juvenile stage, whereas taxa with intermediate or lower reproductive rates are often regulated at later juvenile stages (i.e., birds and small mammals) or by changes in fecundity (i.e., large mammals) (Sinclair 1989).

While many fish populations are dominated by harvest, the imposition of harvest restrictions provides an opportunity to assess the natural processes regulating populations as they recover from overexploitation and the life stages at which they occur. The bull trout (*Salvelinus confluentus*) population in Lower Kananaskis Lake, Alberta, provides a unique opportunity to examine the processes of population regulation over a broad range of densities, as a species with complex life history recovers from heavy overexploitation. In general, many bull trout populations have declined in abundance and distribution in the last century because of overexploitation and habitat deterioration (see articles within Mackay et al. 1997; Rieman et al. 1997; Post and Johnston 2002). Bull trout are currently listed as a threatened under the Endangered Species Act in the coterminous United States (US Fish and Wildlife Service 2006) and are considered sensitive in Alberta, Canada (Alberta Sustainable Resource Development 2001). The bull trout population in Lower Kananaskis Lake is no exception and was in decline from 1947 until 1992, primarily because of overfishing (Stelfox 1997). This species is highly vulnerable to angling because of their opportunistic feeding behaviour and because they attain a catchable size several years prior to maturity (Paul et al. 2000, 2003; Post and Johnston 2002). By 1992, the spawning population was depressed to 60 spawning adults, at which time fishing regulations were changed to zero harvest.

We monitored numerous life stages over a 12-year period to study the demography of recovery of this severely overexploited population and to identify processes of population

regulation. The objectives of this study were (i) to assess what the demographic response of this population was to the reduction in harvest mortality from angling and (ii) to determine what life stage(s) limit population growth. By understanding the processes that influence bull trout population dynamics, better management strategies may lead to the conservation of this species.

Materials and methods

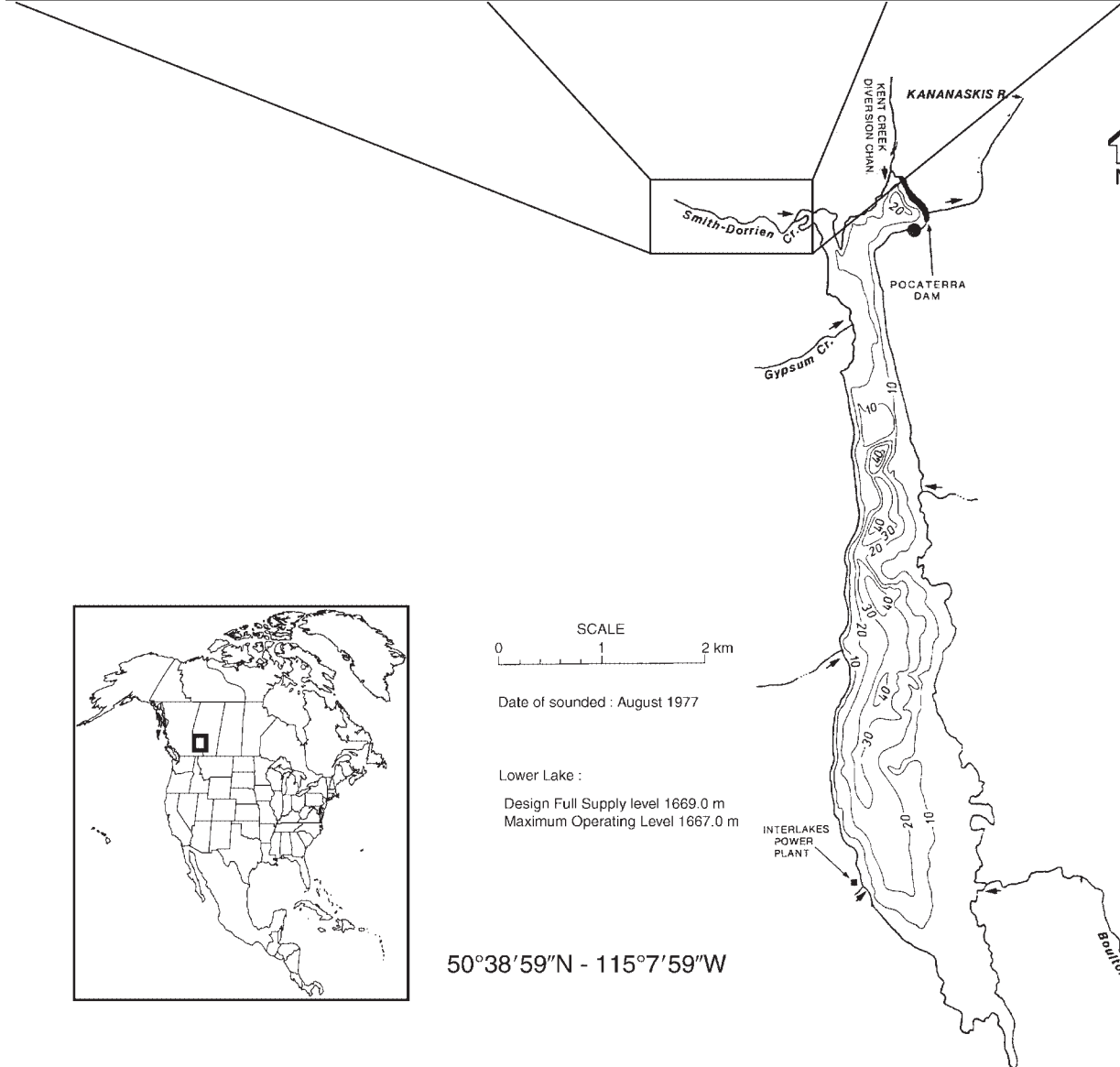
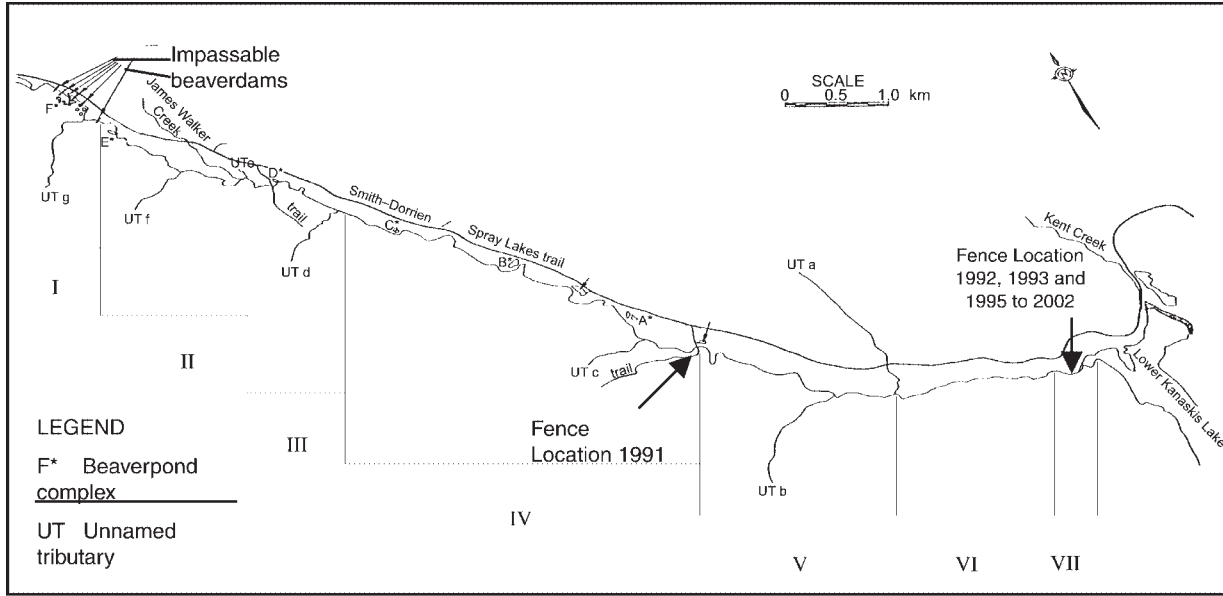
Study area

Lower Kananaskis Lake is a 646 ha reservoir located in Peter Lougheed Provincial Park, Alberta, Canada, at 1667 m above sea level (Fig. 1). Prior to the dam's construction in 1955, Lower Kananaskis Lake supported self-sustaining populations of native bull trout and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) (Stelfox 1997). The dam isolated these fish populations and destroyed potential spawning habitat, leaving Smith-Dorrien Creek as the only suitable spawning habitat for the native bull trout population in Lower Kananaskis Lake (Fig. 1) (Stelfox and Egan 1995). Smith-Dorrien Creek is 18 km long, but because of impassable beaver dams only the lower 13 km are accessible to bull trout spawners. The stream drains 108 km² and has an average gradient from the first impassable beaver dam to the lake of 13 m·km⁻¹. Average stream width ranges from about 7 m near the first dam to 13 m near the mouth. Stream discharge near the mouth ranges from >7 m³·s⁻¹ in spring (late May to early July) to <1 m³·s⁻¹ in autumn (late September to October) (Mushens 2003).

Prior to 1 April 1992, anglers were allowed a harvest of two bull trout per day (five bull trout prior to 1984) of a minimum size of 40 cm (no size limit prior to 1987), which allowed for the harvest of fish not yet sexually mature. In response to the declining numbers of bull trout, angling regulations for Lower Kananaskis Lake were changed on 1 April 1992. The new regulations introduced a full closure of Smith-Dorrien Creek and the northwest bay of Lower Kananaskis Lake to angling to protect staging and spawning bull trout. In addition, a bait ban and catch-and-release regulations for bull trout were imposed on the rest of Lower Kananaskis Lake.

Life history

The bull trout in Lower Kananaskis Lake spend most of their adult life in the reservoir and migrate up Smith-Dorrien Creek to spawn in the fall. The adfluvial bull trout begin their spawning migration between August and September and remain in the stream anywhere from a week to more than a month, returning downstream between September and early November (Mushens 2003; Johnston 2005). During the spawning event, the females build redds. Fry hatch the following spring and rear in the creek for 1–4 years before moving downstream to the reservoir, remaining there for an additional 3–5 years before attaining sexual maturity (Johnston 2005). Bull trout in Lower Kananaskis Lake reach



maturity at approximately 7 years of age (range 6–9) and are iteroparous (Johnston 2005). However, individuals may not spawn in sequential years (Johnston 2005), henceforth referred to as nonrepetitive spawning.

Field methods

The abundance of three different life stages were monitored during this study: adult spawners, juveniles in the stream, and redds. The spawning population was enumerated in Smith-Dorrien Creek during their migration. A fish fence that funnelled fish into either an upstream- or downstream-oriented trap was installed at the mouth of Smith-Dorrien Creek at the beginning of each spawning season from 1992 to 2002, excluding 1994 when the fence was not installed (Johnston 2005). The fence was generally in place from early to mid-August until mid- to late October to encompass the majority of the spawning migration, making it likely that a fish was caught moving in at least one direction of their migration. Design of the fence, traps, and trapping procedure are described fully in Johnston (2005). The fence was also installed in 1991. However, it was installed at a different site, 5.2 km upstream of the mouth of Smith-Dorrien Creek (Fig. 1). Only the downstream trap was installed in 2001.

Electrofishing was used to assess the relative abundance of juveniles in Smith-Dorrien Creek from 1995 to 2003. Electrofishing was carried out in August to early September when flow rates were suitably low, with the exception of 1995 when it was done in late July. A Smith Root Model 12-B battery-powered backpack electroshocker was used with a pulse frequency of 30 Hz, 4 ms⁻¹, and an output voltage of 600 V. The same 500 m index reach was electrofished using a standard three-pass removal–depletion technique, except in 1995 when 600 m was electrofished. The index reach represents moderate quality rearing habitat and was chosen for its accessibility to electrofishing crews. We assume that juvenile abundance in this section of the stream represents the relative abundance of juveniles over the entire creek. Two sections of Smith-Dorrien Creek, ~1 km in length, were also electrofished in 1991 using the three-pass removal–depletion technique (Stelfox and Egan 1995); however, these areas were not within the section of the stream electrofished from 1995 onward.

Bull trout captured in either the traps or electrofishing were weighed (to the nearest 1 g for adults and 0.1 or 0.01 g for juveniles), fork length (FL) was measured (to the nearest mm), and where possible sex and state of maturity was determined. In most years, all bull trout >400 mm were tagged with individually coded Floy® tags and VI Alpha visual implant tags and had their adipose fin removed to identify them as previously captured individuals. Fish were anaesthetized prior to tagging using either clove oil or tricaine methanesulfonate (MS-222). Replicate marking of individual fish aided in their future identification in the event of tag loss. In most years, fish <400 mm were given individually coded passive integrated transponder (PIT) tags and were given adipose and 1/3 dorsal fin clips. Electrofished juveniles were PIT-tagged and given an upper caudal fin clip. Trapped fish were released above or below the trap in relation to their original direction of travel and after consideration of their reproductive state (i.e., ripe or spent).

Electrofished juveniles were released within the index reach where they were captured.

Redds were counted in Smith-Dorrien Creek throughout each spawning season, from 1990 to 2002. The upper sections of the creek, which were the primary spawning areas (sections I and II in Fig. 1), were examined twice during the spawning season, and redds were counted and marked. At the end of October, redds in the entire 13 km of Smith-Dorrien Creek were counted to obtain a complete census. The same protocol for identifying redds was used in all years. These counts were incomplete in 1990, 1994, and 2002 when lower sections of the creek (Fig. 1, sections V to VII) were not censused. However, these sites were used very little for spawning throughout the study period.

Abundance estimates

Using data collected from trapping, electrofishing, and redd counts, abundance was estimated for first-time spawners, total spawners, total adults, population-level fecundity (i.e., total egg number), juveniles by age class, and redds. Individuals caught in the trap each year are assumed to represent a complete census of the spawning population (except in 2001 when trapping was incomplete). We had to estimate the number of spawners in 2001 from those caught moving in the downstream direction only because we were unable to install the upstream trap. However, we believe that some fish were able to escape over an upstream-directed incline plane (designed to allow for only upstream fish passage) during periods of ice buildup. We estimated this loss rate by trapping and releasing 113 marked upstream migrants and counting the number of these that were subsequently caught returning downstream. The entire 13 km of stream was electrofished at the end of October to confirm these fish had not remained upstream after the trap removal. Of the 113 released upstream, 83 were subsequently recaptured moving downstream. Therefore, our best estimate of spawner abundance in 2001 is the number of downstream migrants multiplied by the ratio 113/83.

Abundance of first-time spawners was the census of sexually mature fish caught in the trap for the first time. Exceptions to this were in 1991, 1992, and to a lesser extent in 1993 because these fish may have spawned prior to the commencement of the study and then, because of nonrepetitive spawning, not returned for a few intervening years. Therefore, these cohorts were excluded from analyses of first-time spawners. By 1995, all nonrepetitive spawners from the period prior to 1991 were likely to have returned. However, the 1995 estimate includes first-time spawners from 1994 when the trap was not installed. The 2001 estimate of first-time spawners was adjusted for fish loss over the incline plane as detailed above, and the 2002 count was negatively adjusted to account for this estimated number of 2001 first-time spawners that were missed in 2001 and returned to spawn in 2002.

The annual abundance of adults alive in the system was estimated by tracking individuals interannually using the timing of their last known capture (i.e., an individual must be alive between first tagging and last capture). As a result, the adult abundance estimate is sensitive to the number of additional years of information available after the year being estimated. The more additional years of information avail-

Table 1. The proportion of estimated adult abundance (mean, minimum, and maximum) that was known after the spawning event (represented by zero additional years of data) and 1 to 3 additional years of information.

Additional years of information			
0	1	2	3
0.863 (0.706–0.925)	0.987 (0.977–0.998)	0.996 (0.990–0.999)	0.999 (0.997–1.000)

Table 2. The recruitment models fit to several life-stage intervals to examine density-dependent recruitment and survival of bull trout, *Salvelinus confluentus*.

Model description	Model	Parameter definition
Linear: density independent	$R = pS$	R = abundance of recruits in the resulting life stage; p = proportion of the cohort surviving to recruit; S = abundance of initial life stage (i.e., egg abundance)
Beverton–Holt: compensating density dependent	$R = (kS)/(h + S)$	k = maximum number of recruits produced; h = cohort size required to produce half of the maximum number of recruits
Ricker: overcompensating density dependent	$R = aSe^{-bS}$	a = recruits per unit stock at low stock levels; b = rate of decrease in recruits per unit stock as stock size increases

Note: Models are as described in Haddon (2001).

able, the more accurate the estimate of adult abundance, since the probability of recapturing nonrepetitive spawners increases with subsequent years. This time-series bias was addressed by calculating how much information was gained from each additional year of data. Nonrepetitive spawners were found to miss a maximum of 4 years in a row between spawning events. However, of all known nonrepetitive spawners during the period 1995–1999, 93.5% of these fish only missed 1 year of spawning before they returned to spawn again, 4.3% missed 2 years, 1.7% missed 3 years, and 0.4% missed 4 years. Therefore, one additional year of information was substantial but the value of each additional year after the first declined rapidly. Table 1 presents the proportion of the estimated actual population that was known after each additional year of information was added. The mean (from 1995 to 1999) was used to estimate the adult population size, with the minimum and maximum used to present uncertainty associated with the time-series bias.

In addition to estimating the total adult population size based on assumptions about time-series bias and nonrepetitive spawning, a discrete logistic population growth model was fit to the census data for 1991–1993 and 1995–2000 to obtain estimates for 2001, 2002 and the carrying capacity of the system:

$$(1) \quad N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right)$$

where N_{t+1} is the population size one time step in the future, N_t is the current population size, r is the discrete growth factor or maximum intrinsic rate of increase, and K is the asymptotic size of the otherwise referred to carrying capacity (Gotelli 1998). The discrete logistic population growth model was fit to the data using maximum likelihood analysis with the assumption of normally distributed residuals, and likelihood profiles were used to calculate 95% confidence intervals (CIs) around the parameter estimates (Hood 2004).

Population-level fecundity, measured as total egg deposition, was estimated from measured FLs of spawning females captured at the trap and a FL minus individual fecundity (E ;

eggs per female) relationship established for Lower Kananaskis Lake (Johnston 2005).

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

$(N = 26, r^2 = 0.78, p < 0.0001)$

The estimate of population-level fecundity was adjusted for any ripe female mortalities that were found, for any females that returned downstream without spawning, or for females that were stripped from hatchery purposes (this occurred in 1999 and 2002).

Abundance of each age class of juveniles in the index reach of Smith-Dorrien Creek was determined by length–frequency analysis. Normally distributed age classes were fit to length–frequency distributions using maximum likelihood estimation of a multinomial distribution (Haddon 2001). Individual fish were assigned an age based on a conditional probability function as outlined in Paul et al. (2000). Precision was assessed by comparing ages determined by this technique and ages obtained from otoliths or fin rays of incidental mortalities. Paired sample t tests in SAS[®] were used to determine if results from the two aging techniques differed significantly ($p < 0.05$) (SAS Institute Inc. 2001).

Analysis of density-dependent survival

Three different intracohort recruitment models were fit to data on interannual cohort abundance using maximum likelihood methods. The three models are linear, compensating density dependence, and overcompensating density dependence (Table 2). Residuals were assumed to be log-normally distributed to allow for occasional large recruitment events, such as might occur under optimal environmental conditions (Hilborn and Walters 1992; Haddon 2001). All models run through the origin making the assumption that there was no recruitment without stock, a reasonable assumption because of the absence of immigration or emigration in the system (Hilborn and Walters 1992). Likelihood profiles were used to calculate 95% CIs around parameter estimates (Hood 2004). The small-sample-corrected Akaike information criterion (AIC_c) (Burnham and Anderson 1998) was used to

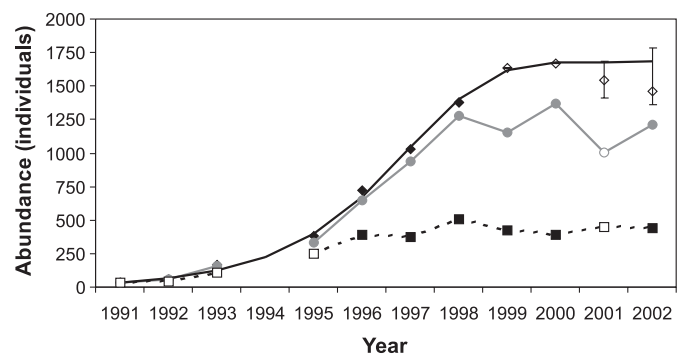
determine the most parsimonious model of the three candidates.

Recruitment models (Table 2) were fit to several life-stage intervals. Recruitment from the egg stage into the adult population was analysed. Maturity was assumed to occur at age 7 for this analysis. Survival of juveniles was then examined over shorter time steps (egg to age-1, age-1 to age-2, and age-2 to age-3) to determine the life stage where density dependence occurred.

To determine the potential influence of abiotic factors on juvenile recruitment in Smith-Dorrien Creek, mean daily autumn discharge (10 August – 10 October) and mean daily water temperature in August were also included in the survival models. These were the abiotic factors for which we had consistent measurements from 1996 to 2002. Both temperature and discharge have been considered to influence the survival of juvenile salmonids either because they occur during sensitive life stages (Jensen and Johnsen 1999) or because they alter habitat selection and resulting competitive interactions (Zorn and Seelbach 1995; Armstrong et al. 2003). High summer temperatures have also been found to decrease juvenile bull trout growth and survival (Selong et al. 2001), and high velocities may alter the efficiency of food capture, therefore affecting growth in salmonids (Armstrong et al. 2003). Using methods outlined in Hilborn and Walters (1992) and maximum likelihood estimation, environmental variables were added individually to the best-fit stock–recruitment model to determine if they improved the fit of the recruitment model. We tested these models with and without a 1-year time lag in environmental conditions. A 1-year time lag examined the influence on survival from environmental conditions in the year previous to capture (the last full growing season). The analysis that did not incorporate a time lag examined the influence on survival from environmental conditions experienced during the census year. Owing to availability of temperature and discharge data (1996–2002) and the time lag, these analyses were performed on two different subsets of the juvenile abundance data used to fit the survival models (1996–2002 for same year comparisons and 1997–2003 for one year lag). As a result, likelihood values are not directly comparable.

Survival of adult cohorts upon reaching maturity was also examined by fitting survival models. This represents intracohort effects and was done for survival from age-7 to age-8 and age-8 to age-9. However, data from 2001 was removed because of the uncertainty of these estimates. In addition, intercohort density-dependent survival to maturity was analyzed by logistic regression in SAS[®] using the Logit link function in PROC GENMOD (SAS Institute Inc. 2001). The survival of adults over a 1-year period as a function of total adult density was examined using this method for the periods 1992–1993, 1995–1996, 1996–1997, 1997–1998, 1998–1999, and 1999–2000, as they represent the periods when adults were no longer vulnerable to angler harvest and there was minimal time-series bias (discussed above and in Table 1). In addition, the proportion of first-time spawners that survived to their second year of maturity was examined as a function of total adult density. This analysis was done to determine if the observation of density dependence in adult survival was simply a function of senescence in a population

Fig. 2. Abundance of the adult population (solid diamonds), all spawning (grey circles and line), and first-time spawning (solid squares and broken line) bull trout, *Salvelinus confluentus*, in Lower Kananaskis Lake during the study period (1991–1993 and 1995–2002). The solid black line indicates predictions from the logistic population growth curve of adult population abundance. Open symbols from 1999 to 2002 indicate values that have been corrected for the bias associated with their occurrence near the end of the study and in 2001 for an incomplete census. The error bars indicate estimated minimum and maximum values calculated from bias corrections related to spawner return rates. Open symbols of first-time spawners prior to 1996 indicate cohorts that may have been overestimated because information on when these fish first spawned is limited to the years studied. However, the reduction of these estimates would only strengthen the recovery relationship.



that was allowed to age once released from harvest mortality.

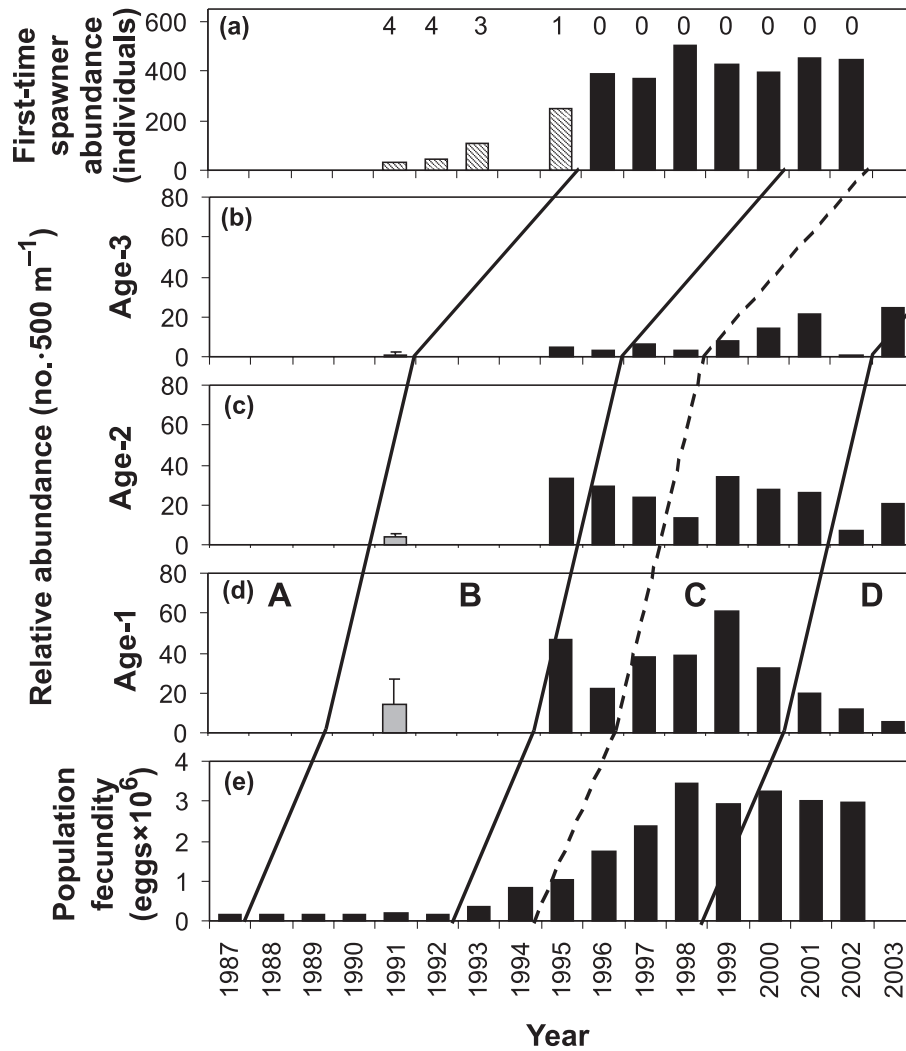
Results

Population abundance

Since 1992, the abundance of spawners, adults, and first-time spawners has increased (Fig. 2). The number of spawners experienced a >20-fold increase during the study period, fluctuating around an asymptote after 1998. The adult population in Lower Kananaskis Lake increased by almost 28-fold from 60 individuals in 1992 to over 1650 individuals by the year 2000, where it also appears to have reached an asymptote. Maximum likelihood analysis of the discrete logistic model fit suggests that the carrying capacity of the adult population is 1680 (95% CI 1635–1729) individuals. The intrinsic rate of increase is estimated to be 0.91 year⁻¹ (95% CI 0.89–0.93). Similar to the adult population, the number of adult recruits (first-time spawners) entering the adult population also increased initially but reached an asymptote of ~440 (Fig. 2). However, the asymptote was reached ~3 years earlier for first-time spawners than it was by the total population and occurred when spawner abundance was still rapidly increasing.

Population-level fecundity increased initially and then approached an asymptote in 1998 (Fig. 3). However, juvenile and first-time spawner abundance did not follow a similar trend. Four cohort groups within the recovery process can be delineated (Fig. 3). Group A represents cohorts that were

Fig. 3. Life stage abundance of bull trout, *Salvelinus confluentus*, in Smith-Dorrien Creek and Lower Kananaskis Lake by year. The solid lines track individual cohorts through time and divide the figure into cohort groups that represent different stages of population recovery (identified by the letters A–D). The panels are as follows from bottom to top: (e) population-level fecundity, (d) age-1 relative abundance, (c) age-2 relative abundance, (b) age-3 relative abundance, and (a) first-time spawner abundance. The number of years exposed to legal harvest is indicated by the numbers above the bars in (a). Abundance estimates of age-1, age-2, and age-3 juveniles (b–d) are relative because these values were obtained from a 500 m index reach that was electrofished annually. The only assessment of juveniles in Smith-Dorrien Creek before 1995 was done in 1991 in two nonindex sections of Smith-Dorrien Creek (shaded columns indicate the minimum relative abundance of the two surveys, and the error bars indicate the maximum relative abundance). The hatched bars represent years when first-time spawner abundance is uncertain, because information on when these fish first spawned is limited by the years studied.



present in Lower Kananaskis Lake and therefore vulnerable to angling harvest as juveniles prior to the regulation changes in 1992. An increasing trend in the abundance of first-time spawners was observed for these cohorts and corresponds with a reduction in the number of years that these fish would have been vulnerable to harvest under the pre-1992 regulations. For example, some of the first-time spawners in 1995 would have been in the reservoir for 1 year prior to the regulation changes and may have experienced some angling mortality as a result, whereas recruits in 1993 would likely have been vulnerable for up to 3 years after migrating into Lower Kananaskis Lake.

Low population-level fecundity due to adult harvest from pre-1992 angling regulations occurred for cohorts repre-

sented by group B (Fig. 3). However, despite low fecundity, recruitment into the adult cohort is high and relatively constant during this period. Group C represents cohorts produced when egg abundance began to increase as the spawning population grew. Cohorts, up to the dashed line, may be tracked to adult recruitment. Although there are only 2 years of data during the growth phase, population-level fecundity increased 5-fold; however, a corresponding increase in the number of adult recruits was not observed. Nor does the relative abundance of the age-1 and age-2 cohorts show a corresponding increase despite the 20-fold increase in population-level fecundity experienced by this group. Additional electrofishing data from nonindex sections of the stream in 1991 suggests that age-1 abundance was either

Table 3. Stock–recruitment model fits to data for population-level fecundity and recruitment of first-time spawning bull trout, *Salvelinus confluentus*, and for intervening life stages using maximum likelihood (negative log-likelihood (–LL)) and AIC_c values.

Life stage		Model (no. of parameters)		
		Density independent (1)	Beverton–Holt (2)	Ricker (2)
Egg–recruit	<i>N</i>	8	8	8
	–LL	6.62	–2.07	–1.23
	AIC _c	15.90	2.26	3.94
	ΔAIC _c	13.64	0	1.68
Egg – age-1	<i>N</i>	9	9	9
	–LL	14.47	9.52	8.57
	AIC _c	31.50	25.04	23.15
	ΔAIC _c	8.35	1.89	0
Age-1 – age-2	<i>N</i>	8	8	8
	–LL	6.05	4.66	4.85
	AIC _c	14.78	15.72	16.10
	ΔAIC _c	0	0.95	1.33
Age-2 – age-3	<i>N</i>	8	8	8
	–LL	14.37	12.83	12.84
	AIC _c	31.40	32.06	32.07
	ΔAIC _c	0	0.66	0.67

Note: The most parsimonious models are assigned ΔAIC_c value of zero. The models tested include a density-independent model (linear), a compensating survival model (Beverton–Holt), and an overcompensating survival model (Ricker).

somewhat lower or did not differ substantially for cohorts of group B compared with group C. The abundance of age-3 individuals showed a slight increase or a similar trend for group C. Group D represents cohorts produced when population-level fecundity was high and relatively constant. Age-1 relative abundance during this period either declined or remained relatively constant.

Agreement between the ages assigned using length–frequency analysis versus the aging of boney structures of the fish was 89.3% for juveniles ($N = 131$) and 93.3% for adult mortalities that had been previously captured as juveniles in the stream ($N = 30$). Ages were not found to significantly differ between the two aging techniques for either juveniles or adults ($t_{[130]} = 1.07$, $\alpha = 0.05$, $p = 0.2868$; and $t_{[29]} = 0$, $\alpha = 0.05$, $p = 1.00$, respectively). This suggests that the age designation based on length gives a reasonable estimate of the age structure of the juveniles captured by electrofishing.

Redd abundance was directly related to the number of females that spawned ($N = 10$, $r^2 = 0.95$, $p < 0.001$). This relationship was not found to differ significantly from a 1:1 relationship (i.e., slope = 1, intercept = 0) ($N = 10$, $r^2 = 0.001$, $p = 0.937$), suggesting that the redd–female abundance relationship remained constant throughout the 20-fold increase in spawner population size.

Density-dependent survival

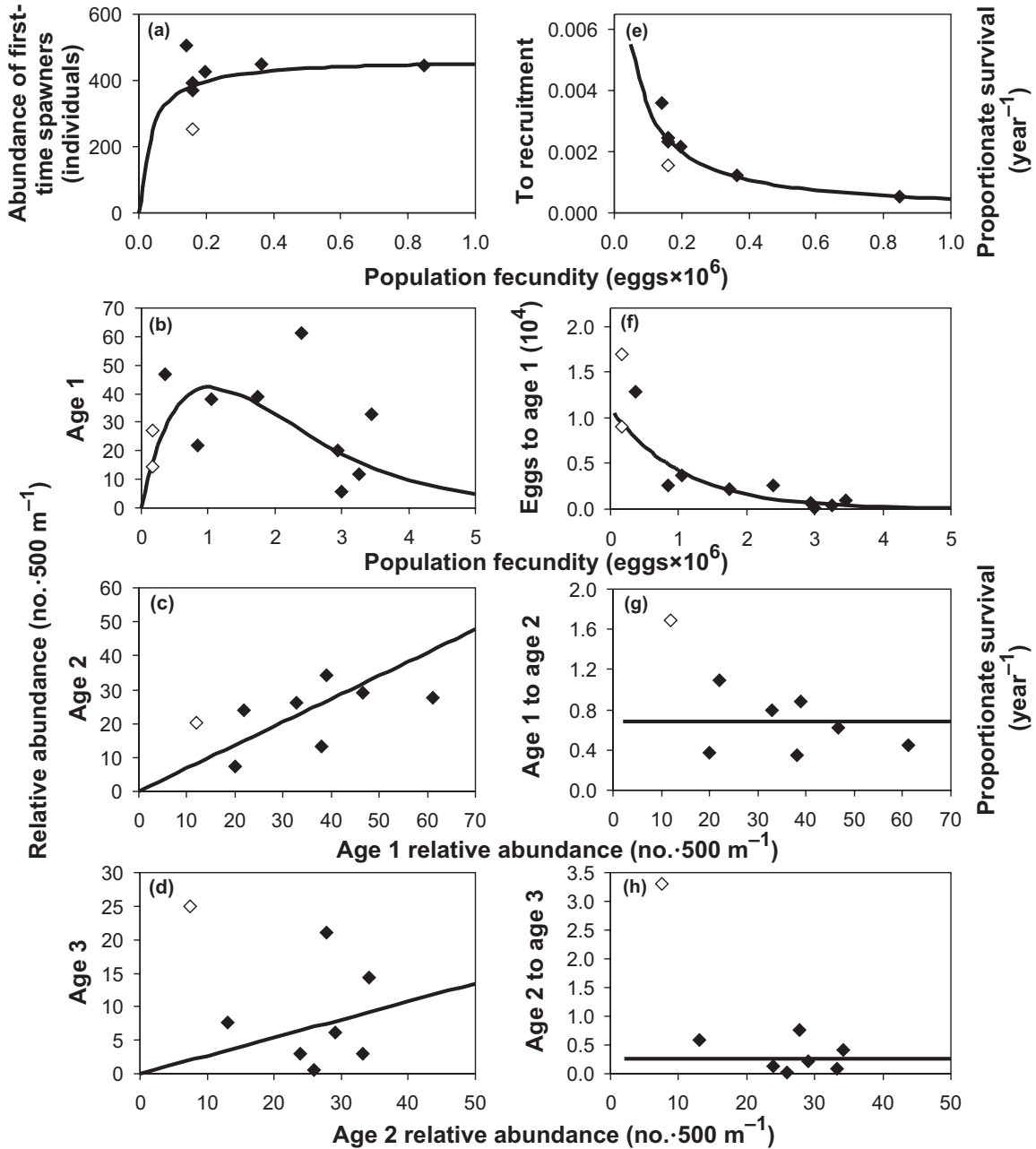
Survival of bull trout from the egg stage to age-at-maturity was found to be density dependent (Table 3). The compensatory Beverton–Holt model was found to be most parsimonious with a >5-fold range in survival across the observed range of abundance and a predicted asymptote of 466 fish (95% CI 307–763) (Figs. 4a and 4e). The ΔAIC_c for the overcompensating Ricker model was less than two, therefore

it could not be rejected (Table 3). However, the difference in AIC_c values between the density-dependent models and the density-independent model was >8 (Table 3), suggesting that some form of density dependence did influence survival from the egg stage to age-at-maturity.

Survival of juveniles was examined by age class to identify when density-dependent regulation occurred. It should be noted that juvenile abundance estimates indicate relative abundance, not a measure of absolute abundance, and older age classes may be influenced by migration (Mushens 2003). Survival rates are the result of both mortality and emigration. Survival from the egg stage to age-1 was found to be density dependent (Table 3). The Ricker model was the most parsimonious; however, based on AIC_c values, the Beverton–Holt model could not be rejected. The density-independent model was rejected (Table 3). Linear regression results of the linear form of the Ricker relationship support this result ($N = 9$, $F_{[1,7]} = 18.92$, $\alpha = 0.05$, $p = 0.003$, $r^2 = 0.73$). This model also appears to be consistent with data collected on juvenile abundance in nonindex reaches in 1991 (Figs. 4b and 4f). Results suggest that the relative proportion of eggs surviving to age-1 appears to be decreasing at a decelerating rate (Fig. 4f).

The pattern differed for survival from age-1 to age-2 and from age-2 to age-3 (Figs. 4c, 4d, 4g, and 4h). The density-independent model was found to be the most parsimonious model (Table 3), a result that was strengthened when the 2003 data point was removed from the data set (ΔAIC_c density-independent model = 0, Beverton–Holt model = 3.88, Ricker = 3.85 for survival from age-1 to age-2; ΔAIC_c density-independent model = 0, Beverton–Holt model = 3.78, Ricker = 3.97 for survival from age-2 to age-3). Electrofishing uses cumulative measures of fish removed to estimate actual population size (Hilborn and Walters 1992).

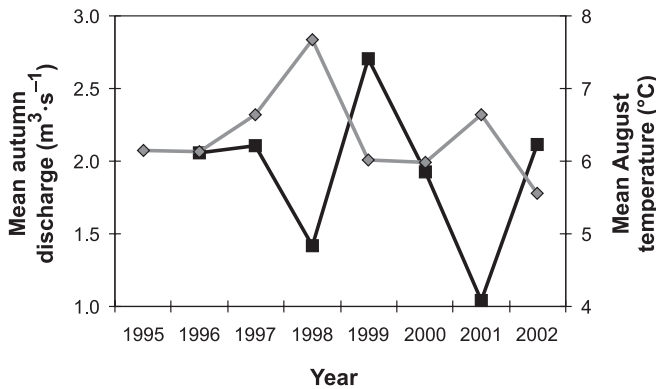
Fig. 4. (a–d) Stock and recruitment relationships among bull trout, *Salvelinus confluentus*, life history stages. The lines are predictions from the best-fit models, and the points represent the empirical data. (e–h) Density-dependent survival calculated from the data and model fits (a–d). The open diamonds in panels a and e indicate values from 1995, a cohort that was potentially vulnerable to angler harvest as juveniles and also includes fish that matured in 1994 when the trap was not in place. However, a reduction in the estimate of first-time spawners in 1995 would only strengthen this relationship. The open diamonds in panels b and f indicate the abundance of juvenile bull trout electrofished in 1991 in two nonindex sections of Smith-Dorrien Creek. The 1991 data were not utilized to fit the stock–recruitment models. The open diamonds in panels c, d, g, and h represent 2003 when the juvenile population did not deplete over three passes.



This was a successful technique, except in 2003 when the population did not deplete over the three passes. The finding that recruitment was not density dependent was further supported by linear regression analyses of both age-1 to age-2 and age-2 to age-3 survival, in which the linearized Ricker curve was not significant either with or without 2003 data included ($N = 8$, $F_{[1,6]} = 2.10$, $\alpha = 0.05$, $p = 0.197$, $r^2 = 0.26$ for age-1 to age-2 survival; $N = 8$, $F_{[1,6]} = 2.80$, $\alpha = 0.05$,

$p = 0.145$, $r^2 = 0.32$ for age-2 to age-3 survival). Therefore, survival of juveniles was found to be influenced by density dependence during the egg stage to age-1, but not during older juvenile stages. There was a 1.6 m³·s⁻¹ range in mean daily autumn discharge and a 2.1 °C range in mean August temperature over the 7- to 8-year period recorded (Fig. 5). Adding mean autumn stream discharge or mean August water temperature with or without a time lag did not improve

Fig. 5. Mean autumn discharge and mean August temperature over the study period. Mean autumn discharge is the mean daily discharge from 10 August to 10 October (solid squares and line). Mean August temperature is the mean daily water temperature in the month of August (shaded diamonds and line).



the fit of the density-dependent or density-independent recruitment models (Table 4).

Survival of adult bull trout in Lower Kananaskis Lake was negatively density dependent, with lower survival of males than females ($N = 5204$, $\chi^2 = 53.16$, $\alpha = 0.05$, $p < 0.0001$) (Fig. 6a). We cannot, a priori, reject the hypothesis that this observation is due to an aging population in which annual survival declines with age. Therefore, we also assessed the survival rate of adults within their first year after spawning, which shows the same pattern of density dependence ($N = 1942$, $\chi^2 = 53.46$, $\alpha = 0.05$, $p < 0.0001$) (Fig. 6b), suggesting that the process is density, not age dependent.

Discussion

The bull trout population in Lower Kananaskis Lake was monitored over a 12-year period to assess the rate of recovery and the demographic processes involved following elimination of legal harvest. The low competitive environment produced from overexploitation should encourage the rebuilding of a population because of compensatory effects (Walters and Kitchell 2001). However, some severely overharvested fish populations have shown a poor ability to rebuild after harvest closures (Hutchings 2000). Recruitment overfishing may deplete spawner abundance below sustainable levels, leading to population collapse (Myers and Barrowman 1996), and compensatory processes and Allee effects may prevent population recovery (Shelton and Healy 1999; Frank and Brickman 2000). However, not all populations or species are equally vulnerable to these processes (Post et al. 2002). We found no evidence of compensatory processes operating in the Lower Kananaskis Lake bull trout population, despite being suppressed to <5% of the unfished equilibrium density. The abundance of adult bull trout began to increase as soon as regulations were changed and grew to an unfished equilibrium population in fewer than two generations. This suggests that the population was growth overfished, not recruitment overfished. The population still had sufficient numbers of sexually mature fish to produce enough recruits to replace those removed by mortality (Haddon 2001). The lack of evidence for compensatory effects is consistent with results from a study by Myers et al. (1995), in which they

found only 3 out of 128 fish populations examined displayed significant depensation. However, it could be that the Lower Kananaskis Lake bull trout population was not depressed sufficiently to exceed the threshold required to observe compensatory effects (Myers et al. 1995; Shelton and Healy 1999; Post et al. 2002). The ability for this population to rebuild begs the following questions: how close to the threshold of collapse was this population pushed and what are the demographic and genetic implications of this?

We were able to examine the demographics of the recovery process by incorporating predictions from the stock-recruitment models with empirical data to track cohort groups over time and through their various life stages. We will use Fig. 7 to clearly illustrate this (labelling corresponds with the same groups presented in Fig. 3). Owing to their use of two distinct habitats during their complex ontogeny, population bottlenecks may occur at a variety of bull trout life stages. These include the following: the egg stage, where spawning habitat could be limiting; the juvenile stage, where rearing habitat may be limiting; and the adult stage, where adult habitat may be limiting. Assessment of the recruitment and survival across life stages demonstrated that both density-dependent and density-independent processes were important in regulating the population.

Early in the recovery process, exposure of juvenile and adult cohorts to harvest mortality was the dominant factor limiting adult abundance. The increase in number of fish maturing when juveniles were exposed to shorter periods of angling harvest under the pre-1992 regulations provide support for this hypothesis (Group A, Fig. 7). Similarly, a rapid increase in adult and spawner abundance occurred once mature cohorts were released from harvest mortality (Group C, Fig. 7). It is not surprising that angler harvest is likely what limited the adult population abundance, when it is estimated that 70% of the fish legally harvested in the winter of 1991–1992 were sexually immature and that 50% of the adult population was harvested during the same period (Stelfox 1997). In contrast, the annual mortality rate for the adult population dropped to 5% during the 1992–1993 period (0% for first-time spawners) once regulation changes were implemented. Long-lived and late-maturing species are often unable to support high levels of mortality (Hilborn et al. 2003), and harvesting fish prior to maturity substantially increases the probability of population collapse (Myers and Mertz 1998). However, compensation primarily during the early life stages prevented collapse from occurring. Despite low levels of egg production because of adult exposure to harvest mortality, maximum numbers of first-time spawners were produced (Group B, Fig. 7). First-time spawner cohorts were no longer directly limited by harvest and, as a result, were characterized by relatively constant recruitment near the asymptote predicted by the Beverton–Holt model.

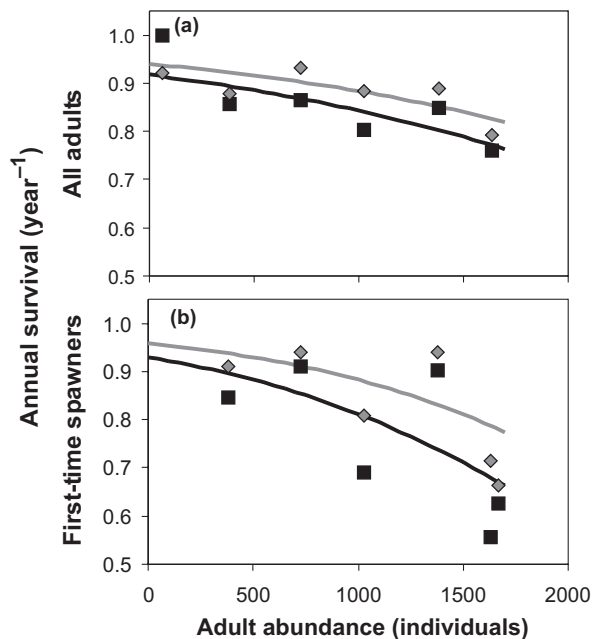
Density-dependent survival during the earliest of the juvenile stages, between eggs and age-1, was found to regulate recruitment into the adult population throughout the recovery process. This is clearly demonstrated by Group C (Fig. 7), where no corresponding increase in age-1 abundance occurs despite an over 20-fold increase in egg abundance that occurred when adults were released from harvest pressure. Our observations are consistent with others studies that concluded that density-dependent survival occurred at

Table 4. The relationship between juvenile bull trout, *Salvelinus confluentus*, survival and environmental factors in the year of sampling and the year prior to sampling.

Life stage		Stock–recruitment model + environmental factor					
		Only stock–recruitment		Mean fall discharge		Mean August temperature	
		No lag	Lag	No lag	Lag	No lag	Lag
Egg – age-1	<i>N</i>	7	7	7	7	7	7
	–LL	6.83	4.07	6.77	3.51	5.26	3.94
	AIC _c	20.65	15.13	27.54	21.02	24.52	21.89
	ΔAIC _c	0	0	6.88	5.89	3.87	6.75
Age-1 – age-2	<i>N</i>	6	6	6	6	6	6
	–LL	5.75	3.71	5.71	3.48	5.38	3.69
	AIC _c	14.30	10.22	18.43	13.97	17.75	14.37
	ΔAIC _c	0	0	4.13	3.75	3.46	4.16
Age-2 – age-3	<i>N</i>	6	6	6	6	6	6
	–LL	9.79	7.10	8.82	7.09	9.78	6.68
	AIC _c	22.57	17.19	25.65	22.18	27.55	21.36
	ΔAIC _c	0	0	3.08	4.99	4.98	4.17

Note: Mean autumn discharge is the mean daily discharge from 10 August to 10 October. Mean August temperature is the mean daily water temperature in August. Environmental variables were added individually to the best-fit stock–recruitment model (i.e., Ricker for egg to age-1 and the density-independent (linear) model for age-1 to age-2 and for age-2 to age-3). Negative log-likelihood (–LL) values were calculated independently for a 1-year time lag and no lag. These analyses are not directly comparable, as they required the use of different data sets.

Fig. 6. Density-dependent survival, by gender, of (a) all adult bull trout, *Salvelinus confluentus*, and (b) adult bull trout in their first year of maturity in Lower Kananaskis Lake. Panel a describes the survival of all adults over the annual periods 1992–1993 and from 1995–1996 to 1999–2000 ($N = 5204$). Panel b describes the survival for first-time spawners only, including the annual periods from 1995–1996 to 1999–2000 ($N = 1942$). The solid squares represent male survival and the shaded diamonds female survival. The black and shaded lines indicate the predicted survival for males and females, respectively, from logistic regression analyses.

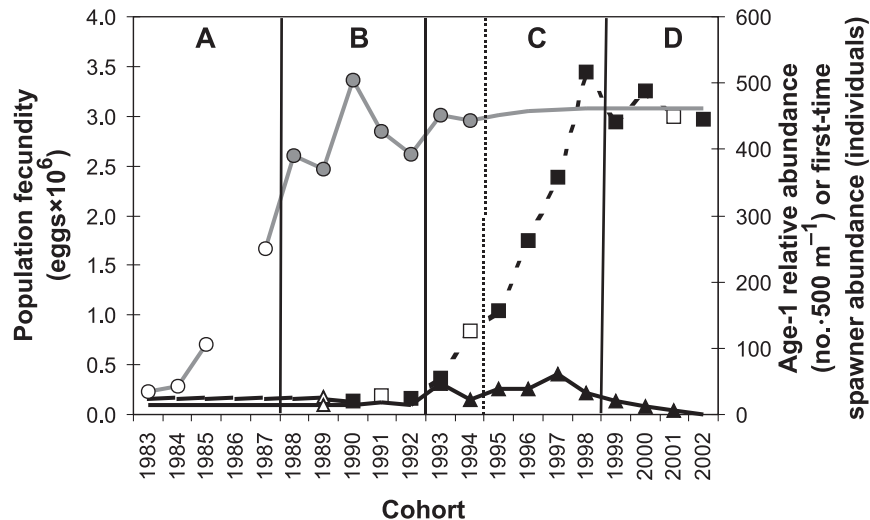


the early juvenile stage followed by constant survival at later stages (Sinclair 1989 and references therein; Elliott 1994; Einum and Fleming 2000); this demonstrates the need for

long-term studies to understand the relationship between juvenile and adult numbers (Shea and Mangel 2001). We were unable to determine on a finer temporal scale when these compensatory processes occurred (i.e., the egg-laying stage, the incubation stage, or the emergence and early rearing stages). However, it has been proposed that density-dependent population bottlenecks usually occur when there is some type of niche shift or developmental shift, such as fry emergence or sexual maturity (Elliott 1994). For example, Einum and Fleming (2000) found that the majority of mortality of brown trout (*Salmo trutta*) fry occurred in the first 4 months after emergence. When examined more closely, developmental or niche shifts often provide insight into the mechanisms that give rise to density-dependent regulation. These mechanisms were not examined explicitly in this study; however, it is worthwhile to discuss possible reasons for the dynamics observed, as it provides avenues for understanding and future research.

The mechanisms behind density dependence can be varying and complex, linking behaviour, growth, and resource allocation. Armstrong et al. (2003) provides a good review of a variety of factors that may affect salmonids and how these factors might interact. Competition for spawning habitat is one possible mechanism regulating age-1 abundance. However, redd abundance was not found to differ significantly from the number of females that spawned, suggesting spawning habitat availability was likely not limiting the growth of this population. Although redd superimposition was observed in the latter years of the study (Johnston 2005), if females were experiencing increased competition for redd sites at higher spawner density, these effects would not have been seen in adult recruitment until after the study was finished. However, no assumption can be made about the quality of the habitat that redds were found in, nor the success of broods from these different habitats. The failure of all broods other than those located in prime spawning habitat could be a mechanism behind the density-dependent

Fig. 7. Empirical estimates and model predictions for population-level fecundity (solid squares and broken line), the relative abundance of age-1 fish (solid triangles and solid line), and the abundance of first-time spawners (shaded circles and shaded line) in relation to the year their cohort was produced. Therefore, cohorts may be followed vertically rather than diagonally, as was seen in Fig. 3. The solid vertical lines track individual cohorts through time and divide the figure into cohort groups representing different stages of population recovery (identified by letters A–D). The data points indicate empirical data, while the lines in sections without data points represent predictions from the stock–recruitment models, or in the case of population-level fecundity, a conservative estimate. The open squares represent years when the number of females spawning (hence egg abundance) was estimated because of incomplete surveys. The open circles indicate that first-time spawner abundance may be overestimated because of the inclusion of fish that spawned in 1994 (cohort 1987) or fish that spawned prior to the commencement of the study and then displayed nonrepetitive spawning. However, the reduction of these estimates would only strengthen the recovery relationship. The open triangles indicate the abundance of age-1 bull trout, *Salvelinus confluentus*, electrofished in 1991 in two nonindex sections of Smith-Dorrien Creek.



survival from the egg stage to age-1 observed in this system. This was not examined explicitly during this study; however, the coarse gravels required for spawning and incubation (Post and Johnston 2002) were observed in abundance within the creek, and age-1 abundance did not change even when female abundance was extremely low, suggesting that spawning habitat availability was unlikely the mechanism driving the observed density dependence.

Intraspecific competition of juveniles for habitat or resources is another mechanism that may regulate the number of fish a stream can support, either through exploitative and (or) interference competition (Thurrow 1997; Harwood et al. 2002). Many stream-dwelling salmonids show aggressive behaviour and establish territorial hierarchies that may be important in limiting fish density during some periods (Elliott 1990; Nakano et al. 1998; Milner et al. 2003). When territories are filled and density increases, fish may migrate in search of more suitable habitat. Elliott (1994) found that juvenile brown trout in search of territories migrated downstream during a “critical period” (30–70 days after emergence), after which time fish had either died or located an appropriate territory. The length of this critical period increased as density increased because of the number of fish seeking territories (Elliott 1990). Competition for suitable habitat is not an unrealistic mechanism for the regulation in age-1 abundance that we see in this system and could explain the maximum density associated with the stock–recruitment curve. Work by Mushens (2003) on this system indicates that juveniles display a high fidelity to their daytime refuges and suggests that once fish have found suitable

habitat they become much more sedentary in their behaviour. It is further suggested that the availability of daytime refuge habitat may be a key limiting factor for juvenile abundance in this system (Mushens 2003). Paul et al. (2000) also found that there was little emigration of age-1 bull trout at low densities in Eunice Creek, and Nakano et al. (1998) found that competitive interactions were important in population regulation, with bull trout establishing territorial hierarchies even in the presence of other species. However, this type of competition may only predominate under the appropriate conditions (Elliott and Hurley 1998). Abiotic factors such as extreme flow rates may also affect abundance (Zorn and Seelbach 1995; Jensen and Johnsen 1999; Selong et al. 2001), although environmental conditions did not improve the explanatory power of recruitment models in this study. However, this could be due to the lack of extreme changes in the abiotic factors measured or the appropriateness of the factors available.

The importance of competition and territoriality is somewhat complicated when it is examined on both the intra- and inter-cohort levels. Paul et al. (2000) found that age-1 and age-2 survival was negatively correlated with effective density, a measure which provides an index of total consumption, indicating that these cohorts interact exploitatively (Post et al. 1999). It has been suggested that these inter-cohort processes should lead to cycling in age-class abundance (Paul et al. 2000), but we see no evidence of this in the time series of relative cohort strengths of three co-occurring cohorts of juvenile bull trout in Smith-Dorrien Creek.

Predation, or the risk of predation, is another mechanism that is suggested to be important in structuring populations (Elliott 1994; Tonn et al. 1994; Biro et al. 2003). Biro et al. (2003) found that the increased mortality at high densities of age-0+ rainbow trout was linked to increased activity and use of environments where individuals were more vulnerable to predation. Tonn et al. (1994) found that survival of age-0+ crucian carp (*Carassius carassius*) to be negatively related to the abundance of older fish and attributed this either to starvation-induced mortality from competition or to cannibalism. Cannibalism is one of the hypothesized mechanisms producing the reduction in recruitment at high stock densities, as seen in the Ricker model, which best described the survival from egg to age-1 bull trout in this population. Cannibalism does occur in this system. It has been directly observed, and four adults were found that had PIT tags in their systems that had been injected into juveniles (Mushens 2003; Johnston 2005). However, it is unclear if the pressure from cannibalism is sufficient to regulate age-1 abundance in the stream, especially as it is restricted to the spawning season when juveniles and adults overlap spatially in the spawning stream.

In the final stage of population recovery, density-dependent survival of adults is apparent. Proportionate survival from age-1 through the juvenile years produces a constant input of adult recruits (Group D, Fig. 7), which in the absence of angling harvest produces an adult population of ~1680 individuals. This suggests that with an annual recruitment estimate of first-time spawners of 440–465 individuals, the equilibrium adult bull trout annual natural mortality rate is ~26%–28%. The mortality was found not to be solely the responsibility of senescence, since survival of new recruits to their second year of maturity also declined as abundance increased. This suggests that intercohort competition among adults is also important in limiting abundance in this population. In this last stage, it appears that both the creek and lake habitats have reached saturation.

A 28-fold increase in the adult population of bull trout in fewer than two generations in response to elimination of harvest clearly demonstrates the extent of overharvest this population experienced. This rapid demographic response in a relatively long-lived and late to mature species demonstrates that the population was growth overfished not recruitment overfished. However, given that only 17 females spawned in 1991, it is hypothesized that this population was approaching the threshold of recruitment overfishing. This study also clearly demonstrates the life history stages that are regulated through density dependence and highlights the importance of having a data series of sufficient length that incorporates the appropriate stage structure of the population to examine these processes. Compensatory density dependence that occurs between the egg and age-1 stages limits the production of recruits into the spawning population. In addition, compensation in adult survival rates produces a second regulatory stage that results in an apparent carrying capacity of adults in the lake. Intervening life stages show no evidence of regulation. In concert, the density-dependent processes occurring at these two life stages provide demographic compensation for low population size. But clearly the ability of the recreational fishery to overcome these natural compensa-

tory processes, and to severely overharvest populations, is pervasive (Hutchings 2000; Post et al. 2002).

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References

- Alberta Sustainable Resource Development. 2001. The general status of Alberta wild species 2000. Alberta Sustainable Resource Development, Fish and Wildlife Service, Edmonton, Alta.
- Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fish. Res.* **62**(2): 143–170.
- Begon, M., Harper, J.L., and Townsend, C.R. 1996. *Ecology: individuals, populations and communities*. 3rd ed. Blackwell Scientific Publications, Oxford, UK.
- Berryman, A.A., Lima Arce, M., and Hawkins, B.A. 2002. Population regulation, emergent properties, and a requiem for density dependence. *Oikos*, **99**(3): 600–606.
- Biro, P.A., Post, J.R., and Parkinson, E.A. 2003. Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. *Ecology*, **84**(3): 691–700.
- Burnham, K.P., and Anderson, D.R. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag New York Inc., New York.
- Einum, S., and Fleming, I.A. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, **54**(2): 628–639.
- Elliott, J.M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. III. The role of territorial behaviour. *J. Anim. Ecol.* **59**(3): 803–818.
- Elliott, J.M. 1994. *Quantitative ecology of the brown trout*. Oxford University Press, Oxford, UK.
- Elliott, J.M., and Hurley, M.A. 1998. Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a Lake District stream. *J. Anim. Ecol.* **67**(2): 280–286.
- Frank, K.T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. *Can. J. Fish. Aquat. Sci.* **57**(3): 513–517.
- Gotelli, N.J. 1998. *A primer of ecology*. 2nd ed. Sinauer Associates Inc., Sunderland, Mass., USA.
- Haddon, M. 2001. *Modelling and quantitative methods in fisheries*. Chapman & Hall/CRC, Boca Raton, Fla., USA.
- Harwood, A.J., Metcalfe, N.B., Griffiths, S.W., and Armstrong, J.C. 2002. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. *Can. J. Fish. Aquat. Sci.* **59**(9): 1515–1523.
- Hilborn, R., and Walters, C.J. 1992. *Quantitative fisheries stock assessment: choice, dynamics, and uncertainty*. Chapman & Hall, London, UK.

- Hilborn, R., Branch, T.A., Ernst, B., Magnusson, A., Minte-Vera, C.V., Scheuerell, M.D., and Valero, J.L. 2003. State of the world's fisheries. *Annu. Rev. Environ. Resour.* **28**: 359–399.
- Hood, G.M. 2004. PopTools. Version 2.6.2. Available from <http://www.cse.csiro.au/poptools> [accessed 12 January 2004].
- Hutchings, J.A. 2000. Collapse and recovery of marine fishes. *Nature (London)*, **406**(6798): 882–885.
- Jensen, A.J., and Johnsen, B.O. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Funct. Ecol.* **13**(6): 778–785.
- Johnston, F.D. 2005. Demographic and life-history responses of an over-exploited bull trout (*Salvelinus confluentus*) population to zero harvest regulations. M.Sc. thesis, Department of Biological Sciences, University of Calgary, Alta.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* **67**(5): 751–762.
- Mackay, W.C., Brewin, M.K., and Monita, M. (Editors). 1997. Friends of the Bull Trout Conference Proceedings. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary, Alta.
- Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S., and Ladle, M. 2003. The natural control of salmon and trout populations in streams. *Fish. Res.* **62**(2): 111–125.
- Mushens, C.J. 2003. Migration, diel movement and habitat use of juvenile bull trout (*Salvelinus confluentus*). M.Sc. thesis, Department of Biological Sciences, University of Calgary, Alta.
- Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? *Fish. Bull.* **94**(4): 707–724.
- Myers, R.A., and Mertz, G. 1998. The limits of exploitation: a precautionary approach. *Ecol. Appl.* **8**(Suppl. 1): S165–S169.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. *Science (Washington, D.C.)*, **269**(5227): 1106–1108.
- Nakano, S., Kitano, S., Nakai, K., and Fausch, K.D. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environ. Biol. Fishes*, **52**(1–3): 345–355.
- Paul, A.J., Post, J.R., Sterling, G.L., and Hunt, C. 2000. Density-dependent intercohort interactions and recruitment dynamics: models and a bull trout (*Salvelinus confluentus*) time series. *Can. J. Fish. Aquat. Sci.* **57**(6): 1220–1231.
- Paul, A.J., Post, J.R., and Stelfox, J.D. 2003. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *N. Am. J. Fish. Manag.* **23**(1): 109–119.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., and Zeller, D. 2002. Towards sustainability in world fisheries. *Nature (London)*, **418**: 689–695.
- Post, J.R., and Johnston, F.D. 2002. Status of bull trout (*Salvelinus confluentus*) in Alberta. Alberta Sustainable Resource Development, Fish and Wildlife Division, and Alberta Conservation Association, Edmonton, Alta. Wildl. Status Rep. No. 39.
- Post, J.R., Parkinson, E.A., and Johnston, N.T. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecol. Monogr.* **69**(2): 155–175.
- Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries*, **27**(1): 6–17.
- Prout, T., and McChesney, F. 1985. Competition among immatures affects their adult fertility: population dynamics. *Am. Nat.* **126**(4): 521–558.
- Rieman, B.E., Lee, D.C., and Thurow, R.F. 1997. Distribution, status, and likely future trends within the Columbia River and Klamath River basins. *N. Am. J. Fish. Manag.* **17**: 1111–1125.
- SAS Institute Inc. 2001. Version 8.2. SAS Institute Inc., Cary, N.C.
- Selong, J.H., McMahon, T.E., Zale, A.V., and Barrows, F.T. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Trans. Am. Fish. Soc.* **130**(6): 1026–1037.
- Shea, K., and Mangel, M. 2001. Detection of population trends in threatened coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **58**(2): 375–385.
- Shelton, P.A., and Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Can. J. Fish. Aquat. Sci.* **56**(9): 1521–1524.
- Sinclair, A.R.E. 1989. Population regulation in animals. *In Ecological Concepts: the Contribution of Ecology to an Understanding of the Natural World. The 29th Symposium of the British Ecological Society, 12–13 April 1988, London. Edited by J.M. Cherrett.* Blackwell Scientific Publications, Oxford, UK. pp. 197–241.
- Stelfox, J.D. 1997. Seasonal movements, growth, survival and population status of the adfluvial bull trout population in Lower Kananaskis Lake, Alberta. *In Friends of the Bull Trout Conference Proceedings. Edited by W.C. Mackay, M.K. Brewin, and M. Monita.* Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary, Alta. pp. 309–316.
- Stelfox, J.D., and Egan, K.L. 1995. Bull trout investigations in the Smith-Dorrien Creek/Lower Kananaskis Lake system. Report prepared by Fisheries Management Division, Alberta Environmental Protection and by Golder Associates Limited, Calgary, Alta.
- Thurow, R.F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. *Ecol. Freshw. Fish* **6** (1): 1–7.
- Tonn, W.M., Holopainen, I.J., and Paszkowski, C.A. 1994. Density-dependent effects and the regulations of crucian carp populations in single-species ponds. *Ecology*, **75**(3): 824–834.
- US Fish and Wildlife Service. 2006. Species information: threatened and endangered animals and plants. Washington D.C. 20240. Available from: http://ecos.fws.gov/species_profile/servlet/gov.doi.species_profile.servlets.SpeciesProfile?spcode=E065 [accessed 9 August 2006].
- Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* **58**(1): 39–50.
- Whalen, K.G., Parrish, D.L., Mather, M.E., and McMenemy, J.R. 2000. Cross-tributary analysis of parr to smolt recruitment of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **57**(8): 1607–1616.
- Zorn, T.G., and Seelbach, P.W. 1995. The relation between habitat availability and the short-term carrying capacity of a stream reach for smallmouth bass. *N. Am. J. Fish. Manag.* **15**(4) 773–783.