

Stock Productivity, Carrying Capacity, and Habitat Utilization of Thompson River Steelhead, as Estimated from 2001-2012 Juvenile Abundance Data.

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ABSTRACT

Stock-recruitment relationships for steelhead populations can be used to define biological reference points that signal the need for management changes. During 2001-2012 we conducted regular monitoring of age-1+ rainbow trout (*Oncorhynchus mykiss*) parr abundance in steelhead streams of the Thompson River basin, in order to develop adult-to-age-1+ stock-recruitment relationships for the system. Fall standing stocks of steelhead parr in the lower Thompson River and in three tributary basins (Deadman, Bonaparte, and Nicola) were estimated using calibrated night snorkel counts and single-pass electrofishing. Each year a total of 123-159 sites were sampled in 19 reach/habitat type strata representing 480 km of juvenile rearing habitat. Mean detection probabilities for snorkeling and single-pass electrofishing, based on mark-recapture and three-pass depletion electrofishing, respectively, were relatively high (65% and 83%, respectively) and precise ($CV = 0.24$ and 0.20 , respectively), suggesting that both methods provided reliable estimates of parr density in all reaches of the study area when adjusted for sampling efficiency. During 2001-2012, total age-1+ parr standing stocks for the study area as a whole averaged 211,591 fish, and ranged from 158,877 to 247,934 among years. Estimates of parr standing stocks for the study area as a whole were relatively precise, with percent relative error ranging from $\pm 11\%$ to $\pm 17\%$ among years for age-1+. Among tributary reaches, highest parr densities occurred in secondary tributaries, which were of higher gradient, had relatively coarse bed material and smaller channel widths relative to wetted widths, and were less impacted by floodplain agriculture and cattle grazing. Lowest parr densities occurred in lower gradient reaches in larger tributaries characterized by small bed material, a higher proportion of fines, and low structural complexity. Parr abundance was also higher in deep habitats (runs and pools) relative to shallow ones (riffles). At the site level, parr abundance was positively related to substrate coarseness and mean depth, and negatively correlated with distance from the stream mouth. We used brood spawner escapements and age-1+ parr abundance data for 2001-2012 to conduct stock-recruitment analyses for tributary stocks and for the Thompson aggregate as a whole, and to generate estimates of management parameters, although it is important to note that stock-recruitment relationships may be confounded by resident rainbow trout production in the Deadman and Bonaparte systems. Calculated for the recent low marine survival period since 2001, Ricker estimates of average recruits-per-spawner (with recruits expressed as the equivalent number of returning adults in the following generation) at low spawning stock size were 4.5, 5.1, 2.6, and 2.7 for the Deadman, Bonaparte, Nicola aggregate and Thompson aggregate stocks, respectively. Estimated maximum recruits (R_{max}) were 344, 320, 1,013, and 1,481, respectively, for these same populations. Spawning stock sizes associated with maximum sustained yield (S_{MSY}) were 125, 110, 403, and 621 fish, respectively. Under the BC Government steelhead management framework, two management reference points are defined: 1) the Conservation Concern Threshold S_{CCT} which is equivalent to S_{MSY} under long-term average marine survival conditions, and 2) the Limit Reference Point S_{LRP} which is equivalent to the adult stock size expected to produce recruitment sufficient to recover the stock to S_{CCT} in one generation. At estimated long-term average age-1+ parr-to-adult survival since the 1980s, the S_{CCT} estimate for the Thompson aggregate stock was 879 spawners. While uncertainty remains about what monitoring time frame best represents long term average survival, in the interim we feel that the parr data collected during our study support setting the S_{CCT} and S_{LRP} at 1,000 fish and 300 fish, respectively, for the Thompson aggregate stock. The S_{LRP} represents an extreme conservation threshold that, if reached, should be associated with removal of all unnatural mortality and initiation of focused management actions directed at stock rebuilding.

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1.0 INTRODUCTION

Major phylogenetic groups have been suggested for British Columbia *Oncorhynchus mykiss* (McCusker et al. 2000), and a number of recurring ecotypes¹ described (Keeley et al. 2005). Summer-run steelhead, or anadromous *O. mykiss* which enter freshwater on spawning migrations in the summer or early fall, are one such ecotype. Further, within British Columbia summer-run steelhead unique conservation units have been delineated for management and conservation status monitoring (Parkinson et al. 2005). Summer-run steelhead of the interior Fraser River watershed form three conservation units² – Fraser Canyon, Mid Fraser, and Thompson (Parkinson et al. 2005) – that are genetically distinct from the nearest major stock groupings on the British Columbia coast and in the Columbia River system (Beacham et al. 1999). They are ecologically unique in the province, being the only interior summer run steelhead stocks south of the Skeena River system. Steelhead of the Thompson conservation unit are the focus of this report.

As a result of concerns for population status resulting from low escapements and declining ocean survivals in recent years (Smith 1999; Ward 2000; Ahrens 2005; Johnston 2013), and the high value of interior Fraser steelhead for British Columbians, the BC Ministry of Forests, Lands, and Natural Resource Operations (FLNRO) and the federal Department of Fisheries and Oceans (DFO) have introduced conservation measures including catch-and-release regulations, angling closures, and restrictions on commercial and First Nations net fishing effort. Development of steelhead escapement targets has been identified as a priority for effective inter-agency cooperation in steelhead management. Toward this goal, adult steelhead population monitoring methodologies for the Thompson stock, initiated by FLNRO and partner organization Habitat Conservation Trust Foundation (HCTF), have included: 1) adult counting fences, 2) resistivity counters, 3) an area-under-the curve population estimation method for the Nicola system involving visual counts and radio telemetry tracking, and 4) radio telemetry studies to identify population structure, habitat use, and spawning behaviours.

Using simulation models based on stock-recruitment data from BC's Keogh River watershed, Johnston et al. (2000) evaluated the effectiveness of alternative management frameworks for long-term steelhead population conservation. They recommended a framework in which conservation actions (which have been agreed upon in advance) are initiated when spawner abundance crosses reference points that have been derived from the stock-recruitment

¹ Ecotype: a population or group of populations with unique physical and ecological characteristics relative to all other potential ecotypes (De Gisi 2002; Keeley et al. 2005).

² These units are not synonymous with units as they are defined elsewhere: 1) "Conservation Units" (CUs) in Canadian salmon populations, defined as a group of wild salmon "sufficiently isolated from other groups that, if extirpated is very unlikely to recolonize naturally within an acceptable time frame" (Anonymous 2005; Tautz et al. 2012); 2) in the United States, "Evolutionary Significant Units" (ESUs), defined as assemblages of populations that demonstrate a "significant contribution to the evolutionary legacy of the species" (Waples 1995).

relationship. For steelhead in the Thompson River basin, existing estimates of stock productivity and adult carrying capacity (stock-recruitment model parameters) have been based on adult-adult stock-recruitment data (FLNRO, unpublished data), but interpreting these data to derive the management reference points defined by Johnston et al. (2000) has been a challenge because of persistent non-stationarity resulting from shifts and trends in marine survival (Johnston 2013).

In 2001, an annual HCTF-funded survey of juvenile *O. mykiss* abundance in steelhead streams of the lower Thompson River basin was initiated, so that freshwater production, where most of the density dependent survival effects are expected, could be used directly as an index of recruitment rather than subsequent adult recruitment. By utilizing juvenile abundance as the recruitment index, imprecision caused by variable marine survival and harvest could be eliminated in the estimation of recruits.

The ideal measure of juvenile anadromous salmonid production is smolt yield, because all sources of mortality over the freshwater life stage are integrated. There are, however, a number of inherent difficulties in acquiring steelhead smolt production estimates for larger river basins. Reliable adult-smolt stock-recruitment data for North Pacific steelhead stocks are presently limited to the Keogh River and Snow Creek, Washington (Johnson and Cooper 1991; Tautz et al. 1992; Ward 2000), both of which are small coastal streams whose flow regimes are largely influenced by rainfall rather than snowmelt. Stock-recruitment relationships for steelhead stocks in these streams may not accurately reflect those in the lower Thompson River or other large interior watersheds, and extrapolations may not be reasonable. In the interior of British Columbia, high flows during spring snowmelt render traps and counting fences ineffective in all but the smallest tributaries, meaning that it may not be feasible to acquire empirical estimates of smolt yield. Moreover, fry from smaller natal tributaries may move downstream as parr to rear in larger mainstem reaches (Bjornn 1971; Starr 1979), suggesting that smolt trapping in smaller tributaries could underestimate the contribution of these habitats to total smolt production. Sampling young-of-the-year (age-0+ fry, where the “0” equates to the number of winters survived) is more feasible than smolt trapping, but the reliability of fry abundance as an index of carrying capacity is questionable because of evidence of density-dependent survival and ‘bottle-necks’ to freshwater production at later freshwater life-stages (Ward and Slaney 1993).

A potential alternative to monitoring smolt production is to survey age-1+ or older juvenile salmonid (parr) abundance near the end of freshwater residency. Research suggests that for anadromous salmonids that have a lengthy freshwater residence, density-dependent mortality occurs primarily in the first year of life (Elliot 1987; Kennedy and Crozier 1993; Ward and Slaney 1993; Hartman et al. 1996; Whalen et al. 2000). This suggests that the standing stock of parr in a stream could be a reliable surrogate of smolt yield. In several studies of Atlantic salmon (*Salmo salar*) populations, surveys of parr abundance have been used as indices of potential smolt yield (Symons 1979; Evans et al. 1984; Chadwick 1987; Kennedy and Crozier 1993). Parr surveys have also been used for steelhead stock monitoring in streams in Idaho,

Oregon and California (Hall-Griswold and Petrosky 1996; Satterthwaite 2002). In the Keogh River, British Columbia, where smolt abundance has been measured empirically in a counting fence, fry abundance was positively related to brood year spawner abundance, but was a poor predictor of subsequent smolt abundance, whereas parr abundance was a good predictor of smolt abundance (Ward and Slaney 1993).

In order to substitute steelhead parr abundance for smolt production in the Thompson River watershed, we required annual fall standing stock estimates for the lower Thompson River and each of its major tributaries and sub-tributaries. However, methods for sampling steelhead parr and other juvenile salmonids in larger stream environments had received relatively little attention. Multiple-pass electrofishing, the conventional method for assessing juvenile salmonid populations in streams, has two major disadvantages with respect to older age classes and larger rivers. First, the method is very time consuming and resources are often insufficient to allow for the large number of sample sites necessary to address high spatial heterogeneity in fish abundance. Stream fish populations are often highly clumped in their distribution as a result of spawning distribution (Beard and Carline 1991), geomorphic influences such as elevation, channel slope, and stream size (Kruse et al. 1997), habitat variability (Newman and Waters 1984), intercohort competition (Bohlin 1978), and other factors. The second principal disadvantage of electrofishing is that it is frequently impossible to achieve good results for salmonid juveniles in larger streams. Mainstem parr habitats often cannot be enclosed with stop nets without substantial site disturbance, if they can be enclosed at all, and excessive depth and current velocity often severely reduce the effectiveness of electrofishing.

Uncertainty in estimates of population size for entire streams areas can be reduced by increasing the number of sample sites through the use of “rapid assessment” methods (Jones and Stockwell 1995) such as snorkeling counts (Hankin and Reeves 1988; Thurow et al. 2006) or single-pass electrofishing (Jones and Stockwell 1995; Wyatt 2002; Bateman et al. 2005). These rapid methods sacrifice accuracy at individual sites to allow a larger number of sites to be sampled for a given amount of sampling effort. However, converting raw counts obtained from such methods to population estimates requires information about detection probability, or the proportion of the population that is captured or detected during each sampling event. To this end, Hankin (1984) advocated a two-stage sampling design whereby detection probability of a rapid assessment method is estimated at a fraction of sites using a more intensive method, then used to estimate abundance from counts at sites sampled using the rapid assessment method. Mark-recapture and multiple-pass depletion methods have both been used to estimate detection probability of rapid assessment methods for stream-dwelling juvenile salmonids (Hankin and Reeves 1988; Wyatt 2002; Korman et al. 2010a; Peterson et al. 2004).

Given the lack of proven methods for sampling steelhead parr abundance in larger streams, the initial focus of this study was to develop suitable sampling methods. We selected night snorkeling as our primary rapid assessment method (Hagen et al. 2005) because the lower

Thompson River and its tributaries experience low, stable flows and good to excellent water clarity throughout the fall in most years, and can be readily sampled using this approach. During 2003-2005, we conducted mark-recapture experiments at 51 sites in the lower Thompson River basin to estimate detection probability for night snorkeling (Hagen et al. 2010). We substituted single-pass electrofishing in riffle habitats in the smaller tributaries that were too shallow for snorkeling. Three-pass depletion electrofishing was used to estimate detection probability for single-pass electrofishing

In 2012, we conducted the tenth annual survey since 2001 (no surveys occurred in 2007 and 2009) of steelhead parr abundance in the lower Thompson River basin using calibrated night snorkeling and single-pass electrofishing as the survey methods. Similar to previous years, parr abundance was sampled at 153 sites. Parr abundance estimates, taken together with corresponding brood spawner escapement estimates (obtained as part of a separate HCTF project; FLNRO, unpublished data), provide a time series of stock-recruitment data that will continue to grow in future years. Presented within this report are:

- A summary of our previous evaluations of night snorkeling and single-pass electrofishing as rapid assessment methods for estimating steelhead parr abundance in the lower Thompson River basin (see Hagen et al. 2010 for a more detailed assessment).
- A summary of annual juvenile steelhead standing stock estimates and mean lengths by age class, stream and reach for 2001-2012.
- An analysis of site-level habitat characteristics affecting steelhead parr abundance in the lower Thompson River basin.
- An evaluation of spawner-parr stock-recruitment relationships to date for individual tributary populations and for the lower Thompson River aggregate stock including estimation of management parameters (juvenile and adult carrying capacity, and adult stock size at maximum sustained yield) and the uncertainty in these estimates.
- An evaluation of several habitat capability models for estimating steelhead carrying capacity in lower Thompson River streams, based on comparisons with our empirically-derived estimates, and a discussion of factors that may potentially contribute to poor model performance.

2.0 METHODS

2.1 Study area

The study area encompasses the major portion of the lower Thompson River watershed used by steelhead including 125 km of the Thompson mainstem from Kamloops Lake to the Fraser

River confluence (Figure 1, Table 1), and 350 km of habitat in the primary (Nicola, Bonaparte, and Deadman rivers) and larger secondary tributaries (Coldwater River, Spius and Criss Creeks).

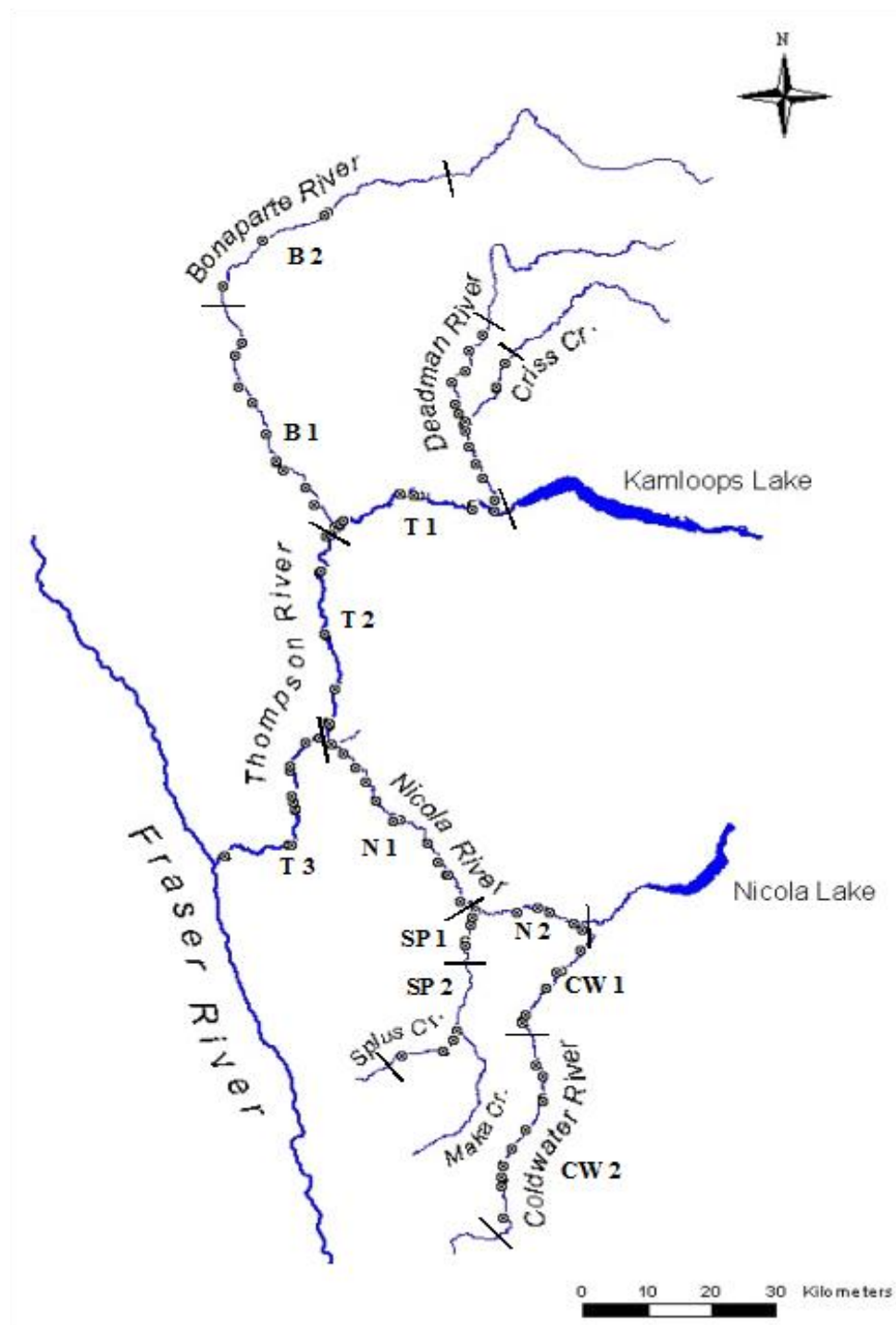


Figure 1. Map of the lower Thompson River basin showing all mainstem and tributary reaches included in the study area. Reach names are given in bold for streams with more than one reach. Reach breaks are indicated by solid slashes and juvenile sampling sites are indicated by dotted circles.

Table 1. Watershed area, stream length currently used by steelhead, stream flow statistics, and mean October wetted widths for the lower Thompson River and its tributaries.

Stream	Stream length		Mean annual discharge (m ³ /s) ¹	Mean October discharge (m ³ /s)	Mean October wetted width (m)
	Watershed area (km ²)	included in study area (km)			
Bonaparte	5020	108	5.7 ²	3.3 ²	12.1
Coldwater	914	79	8.2	2.6	12.1
Deadman	1450	49 ³	3.5	1.1	10.4
Nicola	7280	75 ⁴	27.1	8.2	21.1
Spius	780	39 ⁵	10.4	2.7	12.2
Thompson	-	125	743.4	470.0	98.9

¹ Water Survey of Canada data on file

² Discharge is influenced by a flow-control structure at Bonaparte Lake

³ Includes 12.9 km of Deadman tributary Criss Creek

⁴ Includes only that portion of the Nicola River downstream of the Coldwater River confluence

⁵ Excludes Maka and Prospect Creeks

Four small tributaries to the Nicola River are known to be used by steelhead spawners. These include Nuaitch Creek, with an accessible length of 7.4 km (Tredger 1980a), and Skuhun, Shakan, and Maka Creeks (11, 0.4, and 16 km accessible lengths, respectively; Sebastian 1982). These streams were excluded from the study because of poor access (for sampling) and their likely modest contribution to overall parr abundance in the basin. Minor use by steelhead of other streams, including Prospect, Clapperton and Guichon Creeks, which are tributary to the Nicola River, and Pimainus and Skoonka Creeks, which are tributary to the Thompson River, has been reported in the past (McGregor 1986). However, none of the approximately 200 adults that were radio-tagged over a 4-year period entered these tributaries (FLNRO, unpubl. data), suggesting that their relative contribution to overall steelhead production is also minor and can be disregarded without greatly biasing productivity and carrying capacity estimates.

The lower Thompson River watershed lies within the interior dry belt, and overlaps four biogeoclimatic zones (Krajina 1959): the semi-arid Ponderosa Pine and Bunch Grass zones in the lower elevations areas near the Thompson River mainstem (Nicola, lower Bonaparte, and Deadman rivers), and the Interior Douglas Fir and Montane Spruce zones in the wetter, higher elevation tributaries (Coldwater, upper Bonaparte and Deadman rivers, and Spius and Criss Creeks). Summers are typically hot and dry, and winters cold and dry, although the upper reaches of some tributaries receive substantial snowfalls in winter. In the tributaries the hydrograph is snowmelt driven, with peak flows during the May/June freshet followed by low summer and winter flows, while in the Thompson River, discharge is maintained at relatively

high levels until early fall due to an extensive upper watershed area that includes large lakes and numerous glacier-fed tributaries.

In addition to anadromous steelhead, streams in the lower Thompson River basin support other life history forms of rainbow trout, including resident headwater populations in some tributaries, and also migratory resident fish that spawn in the tributaries and migrate (at some point during the juvenile life stage) to adult rearing habitats in the Thompson River mainstem. Size-at-maturity for migratory fluvial trout ranges from approximately 30 cm to 55 cm (Morris 2002). Radio-tagging studies indicate that steelhead spawn exclusively in tributaries of the lower Thompson River (McGregor 1986), and there is no evidence to suggest that resident trout spawn in the mainstem either. The degree of genetic and demographic independence between steelhead and migratory resident trout in steelhead streams of the Thompson River system has not been evaluated, although this issue is discussed later in the report.

Other salmonids inhabiting the study area include Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), and pink salmon (*O. gorbuscha*), as well as bull trout (*Salvelinus confluentus*), brook trout (*S. fontinalis*), and mountain whitefish (*Prosopium williamsoni*). Largescale suckers (*Catostomus macrocheilus*), longnose dace (*Rhinichthys cataractae*), prickly sculpin (*Cottus asper*), northern pikeminnow (*Ptchocheilus oregonensis*), and red sided shiner (*Richardsonius balteatus*) are also common (McGregor 1986).

2.2 Sampling design

In order to generate juvenile steelhead population estimates for the lower Thompson River study area, we employed a two-stage sampling design (Cochrane 1977). The first stage consisted of sampling a large number of index sites during a single event (night snorkeling count or single pass of daytime electrofishing). The second stage consisted of conducting mark-recapture and three-pass removal experiments at a limited subsample of these sites to quantify snorkeling detection probability and single-pass electrofishing capture probability, respectively. Abundance at each site was estimated by expanding the observed number of fish by the estimate of detection probability. The abundance of fish for a particular stratum (e.g. lower Spius Creek runs) was estimated based on estimates of average fish density and variation in density across sampled sites, and the total standing stock estimate for the stream was the sum of estimates from all sampled strata.

For this type of sampling design, error in the estimation of fish standing stock is the result of both first stage or process error (spatial variation in fish abundance among sampling sites) and second stage or measurement error (error in the estimation of fish abundance within an individual site. Measurement error in the case of snorkeler counts includes variation in detection probability caused by differences in fish behaviour and habitat characteristics among sites, and differences among snorkelers in their ability to spot fish (see section 2.4). With respect to single-pass electrofishing, measurement error includes variation in capture probability among sites and

among individual fish, as well as differences in efficiency among crews (see Section 2.6). We employed a Hierarchical Bayesian Model (HBM) to estimate posterior distributions of the fish standing stocks, from which expected values (mean and median), and 95% credible intervals (Bayesian equivalent of confidence intervals) could be computed (see section 2.7).

Our sampling design also incorporated stratification by reach and habitat type. This is generally an efficient approach to reducing first stage error resulting from strong spatial heterogeneity in fish abundance (Hankin and Reeves 1988), and also allowed us to estimate fish populations for individual streams and reaches within the study area. We initially delineated the study area into 11 reaches during the 2001 pilot study: three reaches in the Thompson River mainstem and eight reaches in the tributaries (Table 2; Figure 1). Reach breaks in the Thompson River mainstem were based on expected differences in habitat quality for parr and proximity to major spawning tributaries. Reach T1 includes the 39 km section of the mainstem from Kamloops Lake to the mouth of the Bonaparte River, reach T2 includes the 57 km section between the Bonaparte River and the upstream end of the canyon section which begins downstream of Spences Bridge, and reach T3 represents the 28 km canyon section which extends downstream to the Fraser River. Kamloops Lake is thought to be the upstream limit to steelhead distribution in the Thompson River mainstem (McGregor 1986, Renn et al. 2001). For Spius Creek and the Nicola River, we delineated upper and lower reaches to reflect observed differences in adult spawner densities (Webb et al. 2000) or apparent suitability for juvenile steelhead rearing (Nicola). Deadman and Criss Creeks and the Coldwater River were each treated as single reaches. The Bonaparte River was formerly treated as two reaches (Hagen et al. 2005), but in this report the two reaches were amalgamated into a single reach based on the lack of a consistent difference in steelhead parr fish densities between the two reaches during 2001-2012. For all streams, we delineated upstream reach boundaries based on the extreme upstream extent of documented adult migration, which was interpreted from Ministry of Environment (MOE) radio telemetry records (Renn et al. 2001) and the professional judgment of MOE staff (S. Maricle, and S. Webb, MOE Kamloops, pers. comm. 2001).

Table 2. Description of habitat stratification, sampling methods, methods for estimating detection or capture probability (see Section 2.2), and sampling intensity (number of sites) for all study reaches in the lower Thompson River basin during 2001-2012. Also shown are total stream length for each stratum, and the mean length of sampling sites averaged across years.

Stream reach	Original habitat type ²	Total length (km)	Sample method	Calibration method	Mean site length (m)	Sample size									
						2001	2002	2003	2004	2005	2006	2008	2010	2011	2012
Bonaparte	riffle	40.3	snorkeling	mark recap.	20	7	8	8	8	NS ¹	8	8	8	8	8
	run	67.5	snorkeling	mark recap.	40	14	16	16	16	NS ¹	16	12	12	12	12
Criss	riffle	7.8	1-pass EF	3-pass EF	14	3	6	6	5	5	6	6	6	5	5
	run	5.0	snorkeling	mark recap.	20	5	8	8	6	8	8	7	8	6	6
Coldwater	riffle	44.1	1-pass EF	3-pass EF	14	8	9	8	8	NS ¹	7	8	8	8	8
	run	34.9	snorkeling	mark recap.	37	16	16	16	15	16	15	15	14	16	16
Deadman	riffle	16.8	1-pass EF	3-pass EF	15	5	5	6	6	6	5	7	7	7	7
	run	19.3	snorkeling	mark recap.	35	10	11	11	11	12	11	9	9	9	9
L. Nicola	riffle	27.8	snorkeling	mark recap.	21	8	9	8	9	9	9	7	3	7	7
	run	22.8	snorkeling	mark recap.	65	11	10	9	9	10	10	8	NS ¹	8	8
U. Nicola	riffle	10.2	1-pass EF	3-pass EF	20	3	3	4	3	4	3	3	3	3	3
	run	13.8	snorkeling	mark recap.	67	5	4	5	6	5	5	4	NS ¹	4	4
L. Spius	riffle	4.4	1-pass EF	3-pass EF	13	4	7	6	7	NS ¹	6	5	6	5	7
	run	2.3	snorkeling	mark recap.	33	5	7	7	7	7	7	6	6	6	6
U. Spius	riffle	19.3	1-pass EF	3-pass EF	14	3	3	3	4	4	4	5	5	5	4
	run	12.9	snorkeling	mark recap.	21	3	4	3	4	4	5	6	6	7	7
Thomp. (T1)	bar	8.3	snorkeling	mark recap.	81	4	3	3	3	3	3	3	3	3	3
	dfs	11.4	snorkeling	mark recap.	82	4	3	3	3	3	3	3	3	3	3
	embay	19.8	snorkeling	mark recap.	69	4	3	3	3	3	3	3	3	3	3
	rapid	0.2	not sampled	-	-	-	-	-	-	-	-	-	-	-	-
Thomp. (T2)	bar	14.4	snorkeling	mark recap.	79	6	4	4	4	4	4	4	4	4	4
	dfs	19.9	snorkeling	mark recap.	85	6	4	4	4	4	4	4	4	4	4
	embay	19.8	snorkeling	mark recap.	73	5	4	4	4	4	4	4	4	4	4
	rapid	2.8	not sampled	-	-	-	-	-	-	-	-	-	-	-	-
Thomp. (T3)	bar	3.6	snorkeling	mark recap.	88	4	4	4	4	4	4	5	5	5	5
	dfs	10.6	snorkeling	mark recap.	85	4	4	4	4	4	4	5	5	5	5
	embay	11.9	snorkeling	mark recap.	81	4	4	4	4	4	4	5	5	5	5
	rapid	2.1	not sampled	-	-	-	-	-	-	-	-	-	-	-	-
Total		474				151	159	157	157	123	158	152	137	152	153

¹Not sampled due to poor survey conditions.

²To model fish standing stocks in this report, we pooled all habitat strata within each reach of the Thompson River mainstem, reducing the number of Thompson River strata from nine to three (see Section 2.2, paragraph 2).

For all tributary reaches we designated two habitat types, riffles and runs, with the latter type including all lower gradient habitats such as pools, runs, glides and alcoves (Table 2). Riffle and run habitat stratification was inappropriate for the Thompson River mainstem reaches, where wetted width exceeds 100 m, parr at night are limited to near-shore areas by high midstream current velocities (>1 m/s), and habitat suitability is determined by shoreline characteristics such as depth, velocity and bank material composition (Beniston et al. 1985). During 2001-2008, we designated three shoreline habitat type strata for the Thompson River mainstem: cobble bars (shallow areas of laminar flow with gravel or cobble substrates that slope gradually away from the bank), deep/fast shorelines (areas with depth greater than 1.0 m and velocity greater than 0.5 m/s within 5 m of the shore), and embayments (shorelines with average water velocities <0.1 m/s, irrespective of other physical characteristics). However, the model validation process for the Hierarchical Bayesian Model (see Section 2.7.2) indicated that sample sizes for individual Thompson mainstem habitat strata were too low (3-5 sites per strata) to reliably estimate variance in abundance. Because there were no consistent differences in juvenile steelhead density among the habitat strata within these reaches, we retained the original reach stratification for the Thompson mainstem in our HBM analysis (see paragraph above), but pooled sample sites from the three habitat strata within each reach (Table 2).

Where available, we relied on previously documented habitat surveys (Tredger 1980b, 1980c; Sebastian 1982) to provide estimates of the total length and area for tributary strata (Deadman, Bonaparte, Nicola). To obtain habitat data for the remaining tributaries (Coldwater, Criss) and the Thompson River mainstem, we conducted habitat surveys during October 2002.

Within each stratum, fish populations were sampled using a systematic sampling design (Cochrane 1977) whereby, in each mainstem or tributary reach, snorkeling sites were distributed at uniform intervals (with some deviations resulting from access limitations). For the tributary reaches, snorkeling sites in run habitat strata consisted of entire habitat units. For riffle strata, habitat units were sub-sampled. This was done because single-pass electrofishing was substituted for snorkeling in riffle strata in the smaller streams, and generally riffles were too long to allow for sampling of entire habitat units. For riffle strata, each site was a minimum of 100 m^2 in area and 10 m in length. For the three habitat types in the Thompson River mainstem reaches, site length equaled the entire length of the unit or 100 m if the shoreline habitat unit exceeded this length.

Physical site attributes recorded during site layout included descriptions of disturbance types, riparian vegetation, channel confinement, substrate composition (boulder, cobble, gravel, and fines as percentages of the site area), D90, D50 (diameters of substrate particles for which 90% and 50%, respectively, of the site area consist of smaller particles), bank composition, length, wetted width, percent cover (categories included: overhead vegetation, turbulence, deep water and boulder as percentages of the site area; undercut bank as a percentage of the combined length of the stream banks, and the total area of wood debris >10 cm in diameter), and average

and maximum thalweg depths (based on 10 measurements, each taken at the deepest point along a cross-channel transect except in the case of the Thompson River, where visually estimated maximum site depths were substituted for thalweg depths).

2.3 Night snorkeling surveys

We used night snorkeling counts at unenclosed sites, adjusted for detection probability, to estimate fish abundance for the majority of the sampling strata in our study area (Table 2). Snorkeling surveys were conducted at night because numerous studies have shown that day concealment behaviour is common in juvenile salmonids (Cunjak et al. 1988; Thurow and Schill 1996; Hillman et al. 1992; Bradford and Higgins 2000 and references therein; Thurow et al. 2006), and likely depends on factors such as temperature, time-of-day, season and habitat. We limited snorkeling counts to a four-hour period beginning 0.5 hours after dusk based on Bradford and Higgins' (2000) finding that, throughout the year, the highest abundances of steelhead parr were observed during the 4-hour period following dusk.

In all streams except the Thompson River mainstem, snorkelers surveyed the stream's entire wetted width. At sampling locations in the Thompson River snorkelers moved out as far as was physically possible from shore or until no fish were observed. To determine if fish were present in the higher velocity mid-channel portion of a Thompson River site where upstream travel was not possible, snorkelers would conduct periodic downstream sweeps. However, this appeared to be generally unnecessary, as juvenile salmonids at night were mostly limited to inshore locations of reduced current velocity.

To illuminate the sampling sites at night, snorkelers used handheld dive lights of the same type in each year. In very clear water or shallow sites, snorkelers frequently diffused the beams by reflecting them off the underside of the stream surface. Snorkelers worked in groups of two, with each crewmember entering the site at its downstream end and systematically sweeping in an upstream direction the area between their bank and the agreed upon mid-point of the site. Regular communication between snorkelers was essential to avoid duplicating counts, particularly in the instances where fish were distributed across the entire wetted width of the stream. In the smallest stream reaches (Criss, Upper Spius), and in the single shoreline habitat units in the Thompson River mainstem, surveys were conducted by a single snorkeler.

The fork lengths of all steelhead juveniles observed that were large enough to potentially be age-1+ or older parr (>75 mm) were visually estimated and recorded in waterproof notebooks, while steelhead smaller than this were tallied as age-0+ fry, without estimates of their lengths. Because counts of steelhead 75-95 mm long included some fry, subsequent length-frequency and scale aging analyses were used to separate fry. To aid in their estimation of fish length, snorkelers drew ruled scales on the cover of their notebooks. Snorkelers were often able to hold the notebooks within 30 cm of a fish to measure its length without disturbing it. In a separate study that employed the same night snorkeling methodology (Decker and Hagen 2009), the

ability of the crew, comprised of several of the same individuals that participated in this study, to accurately estimate rainbow trout parr length was examined by having them estimate the length of each fish prior to attempting its capture during marking events. Results indicated very precise relationships between their estimates and measured fork lengths ($r^2 = 0.94-0.97$), with no consistent positive or negative bias.

2.4 Mark-recapture estimates of snorkeling detection probability

During October 2003-2005, we performed two-pass mark-recapture experiments at 51 sites distributed among seven streams to estimate night snorkeling detection probability. Detailed analysis of the mark-recapture study is presented in Hagen et al. (2010), but the methodology is briefly described below.

On the first night, fish were captured, marked, and released back into the site. On the second night, marked and unmarked fish were enumerated. Detection probability was estimated as the proportion of marked fish that was detected by snorkelers on the second night (recapture event). Previous electrofishing studies have recommended a minimum recovery time of 24 hours to avoid bias in subsequent estimates of detection probability as result of behavioural changes associated with capture and handling (Schreck et al. 1976; Mesa and Schreck 1989; Peterson et al. 2004; Rosenberger and Dunham 2005). We avoided longer recovery periods, as this would likely result in greater numbers of marked fish leaving our open sites (Peterson et al. 2004).

During marking passes, steelhead parr were captured and marked by a snorkeler using two, 27 cm diameter aquarium nets affixed to handles of approximately 80 cm in length. Because minimizing behavioural effects on marked fish was a primary goal of the marking methodology, snorkelers netting parr took care to move cautiously and to avoid chasing fish from their holding locations. Captured fish were handed to a second crew person standing nearby on shore or in the stream who measured each fish's fork length, removed a scale if required for aging analysis, tagged it, and returned it to the location where it was first observed. Captured fish were not anaesthetized because of uncertainty about behavioural effects from the anaesthetic. During later analysis, fish ages were determined by inspecting scales mounted on glass slides using a microfiche reader, with regions of closely spaced circuli on the scale denoting annuli. The best scale for each individual fish was photographed with a digital camera for future reference.

As we were unable to acquire suitable commercially-made tags, we manufactured our own. These consisted of a 10-15 mm-long piece of coloured plastic chenille attached to a size 16, barbed, fine wire fishhook with a short (3-4 mm) length of heat-shrink tubing, 2.1 mm in diameter, and of the same colour as the chenille. Tags were inserted through 3-5 mm of the skin and cartilage along a fish's back at the posterior insertion of the dorsal fin. We used different-coloured tags to differentially mark parr according to fork length category (80-100 mm, 100-170 mm, or >170 mm) to aid snorkelers in correctly assigning resighted marked parr to these categories. We assumed that there was no tag loss or tagging-induced mortality over the 24-hour

period between marking and recapture events. This was supported by a holding experiment where 100 hatchery coho salmon (*Oncorhynchus kisutch*), of a size range similar to age-1+ steelhead parr (90-120 mm), were tagged using the same methods applied for this steelhead study. We observed no tag loss or mortality over the 24-hour duration of the experiment.

Parr populations were treated as effectively closed for the 24-hour period between marking and recapture passes. We evaluated this assumption by having snorkelers survey an additional distance of approximately half the site length upstream and downstream of the original upper and lower site boundaries (i.e. surveyed length was approximately twice the marking site length), and record marked fish observed in these adjacent sections separately.

The analysis of Hagen et al. (2010) identified that snorkeling capture probability varied significantly with parr size, and declined with increasing cross-sectional area of the sampling sites. To account for these factors affecting snorkeling capture probability, we treated fish size (3 categories: 80-100 mm, 100-170 mm, or >170 mm) and stream size (2 categories: larger Thompson and Nicola mainstem reaches, or smaller tributary reaches) as additional levels of stratification in the HBM for reach/habitat strata where snorkeling was the sampling method (see Section 2.7.2).

2.5 Single-pass electrofishing

We substituted single-pass electrofishing at stop net-enclosed sites in six riffle habitat strata in small or shallow tributary reaches (Table 2), owing to the fact that these riffles were too shallow to be surveyed by night snorkeling. Single-pass electrofishing catches were adjusted for capture probability to provide an abundance estimate (Jones and Stockwell; 1995; Peterson et al. 2004; Rosenberger and Dunham 2005). Electrofishing sites in riffles were fully enclosed (one bank to the other) by upstream and downstream stop nets. Electrofishing was initiated at the downstream net, and consisted of a thorough search in an upstream direction, followed by a systematic sweep back towards the downstream net. For the relatively wide (>20 m) upper Nicola reach, where riffles were sampled at sites along one shore, upstream and downstream stop nets were placed perpendicular to the shore and the offshore side of the site was bounded by water too swift to be utilized by parr. At these sites, a series of electrofishing sweeps were conducted, each one commencing at the offshore boundary and moving towards the shore, to avoid chasing larger juveniles from the site.

All salmonids captured during electrofishing were anaesthetized, identified as to species, measured for fork length (nearest mm), and released back into the site following the completion of sampling. Scale samples were also collected from a portion of the juvenile steelhead captured to assist with aging analysis.

2.6 Three-pass electrofishing to estimate capture probability for single-pass electrofishing

During 2001-2005, three-pass depletion electrofishing was utilized at a subset of the riffle sites in the smaller tributary reaches to provide estimates of capture probability for single-pass electrofishing. Three-pass depletion data were used to compute maximum likelihood (ML) estimates of fish abundance (Otis et al. 1978). Although the potential for negative bias in the depletion estimates exists (Riley et al. 1993; Peterson et al. 2004), for the purpose of estimating capture probability for a single electrofishing pass, ML depletion estimates were treated as ‘true’ abundance estimates. At each three-pass site, capture probability was estimated as the first pass catch divided by the ML depletion estimate. In the HBM, capture probability was modeled separately for “small fish” (age-0+ fry) and “large fish” (age-1+ and age-2+ parr) using discrete three-pass removal data for each group. There was insufficient data to estimate capture probability independently for the two parr age classes.

2.7 Estimation of juvenile steelhead standing stocks

To estimate juvenile steelhead abundance by age class for individual habitat strata, reaches and streams, and for the lower Thompson system as a whole, and to quantify uncertainty in these estimates, we relied on a modified version of a Hierarchical Bayesian Model (HBM) originally developed by Korman et al. (2010b) to estimate juvenile steelhead abundance in the Cheakamus River, British Columbia. Their model is in turn a derivation of a model originally proposed by Wyatt (2002, 2003). The sampling (night snorkeling and single-pass electrofishing) and calibration methods (mark-recapture and three-pass removal electrofishing) employed in the Korman et al. (2010b) study were similar to those used in this study. The hierarchical structure of the HBM approach is well suited to two-stage sampling designs where it is necessary to combine error sources arising at different levels or hierarchies of the sampling design (Wyatt 2002).

As previously described in Section 2.2, our sampling design incorporates stratification by reach and habitat type to address strong spatial heterogeneity in fish abundance. The HBM incorporates this stratification along with additional levels of stratification for fish age class and, for reach/habitat strata that were sampled by snorkeling, for fish size class and stream channel size (see Section 2.4). The HBM incorporates stratification by generating independent standing stock estimates for all strata that are specified in the model input files. In order to generate standing stock estimates for entire reaches or streams, or the study area as whole, the HBM sums estimates across the appropriate strata. In contrast, the mark-recapture (snorkeling) and three-pass removal (electrofishing) data were used to generate detection (or capture) probability hyper-distributions that were applied across all strata where each sampling method was employed. This was appropriate because it was not our intent to collect adequate data to generate unique detection probability distributions for individual strata, reaches or streams. Descriptions of all parameters, variables, constants, subscripts and equations used in the Thompson HBM are provided in Appendices 2 and 3. General details of the model are provided below.

For the observation (detection) component of the Thompson HBM, the number of marked fish observed at snorkeling mark-recapture site i during the recapture event was assumed to be binomially distributed and to depend on the detection probability and number of marks released during the initial marking event (Appendix 3, equation 1). The between-site variation in detection probability at mark-recapture sites was assumed to follow a beta hyper-distribution (equation 4). For the three-pass electrofishing sites, the number of fish captured during each pass at three-pass removal site i was assumed to follow a beta distribution and to depend on the detection probability and number of fish present (equation 2); the variation in detection probability among three-pass removal sites was also assumed to follow a beta hyper-distribution (equation 4). For both snorkeling and electrofishing sites, the number of fish observed at index site j (regular sampling site as opposed to a mark-recapture or three-pass removal site) was assumed to be binomially distributed and to depend on abundance at the site and a randomly selected detection probability taken from the hyper-distribution of detection probabilities (equations 5 and 6). The process component of the Thompson HBM assumes that variation in juvenile abundance across sample sites follows a Poisson/log-normal mixture. That is, abundance within a site is Poisson-distributed with a mean equal to the product of fish density and length of stream that was sampled (equation 7), and the log of fish density across index sites is normally distributed (equation 8).

The total standing stock for an individual stratum (stratum s ; Appendix 3, equation 11) was computed as the sum of the standing stock estimates from sampled sites in the stratum (equation 9) and the standing stock estimate for the unsampled stream length within the stratum (equation 10). The latter value was computed as the product of the back-transformed mean density from the lognormal density hyper distribution (μ_λ) with lognormal bias correction ($0.5\tau_\lambda$), and the length of the unsampled portion of the stratum. Standing stock estimates for individual streams were obtained by summing across the appropriate strata-specific estimates (equation 12), while the standing stock estimate for the entire Thompson River system was obtained by summing across all strata-specific estimates (equation 13).

Posterior distributions of parameters and standing stock estimates from the HBM were estimated using WinBUGS (Spiegelhalter et al. 1999) called from the R2WinBUGS library (Sturtz et al. 2005) from the “R” statistical package (R Development Core Team 2009). Uninformative prior distributions for hyper-parameters were used whenever possible for habitat-, reach-, age-, and size-specific strata. As well, an uninformative uniform prior was used for both the mean and standard deviation of the hyper-distribution for age-, and size-specific detection probability (Appendix 3, equations 14 and 15). An uninformative normal prior was used for the mean of the hyper-distribution for log fish density, and an uninformative half-Cauchy distribution was used as a prior for the standard deviation of log fish density (equation 16). The half-Cauchy prior, also referred to as a ‘folded t distribution’, is useful in cases where it is difficult to estimate the variance of hyper-distributions in hierarchical Bayesian models due to limited information in the data (Gelman 2006).

In some cases, estimates of the variance in the hyper-distributions of detection probability or log fish density were unstable based on these uninformative priors. This occurred because the number of mark-recapture (or three-pass removal) experiments or the number of index sites, respectively, was small. In these cases, which are described in the *Results* section, we either used informative normal priors that were parameterized based on the posteriors from another strata with adequate replication, or we estimated a common variance in the hyper-distribution across multiple fish size classes (detection component) or reach/habitat strata (process component). In these cases, the means of the hyper-distributions were still estimated separately for each fish size class or reach/habitat strata. Data deficiencies with respect to parameter estimation are summarized in Appendix 4.

Posterior distributions were estimated by taking every second sample from a total of 10,000 simulations after excluding the first 1000 ‘burn in’ samples. This sample size and sampling strategy was sufficient to achieve adequate model convergence in all cases. Model parameters were estimated in two stages. In the first stage, the posterior distributions of site-specific detection probabilities and hyper-parameters were estimated (equations 3.1 – 3.4). In the second stage, posterior distributions for the parameters in the population model were estimated. The $\theta_{j,g}$ values required for the population model were simulated from beta hyper-distributions whose parameters were determined from the median values of the posterior distributions estimated in the first stage. This two-phased estimation approach reflects our two-stage sampling design, and ensures that the hyper-distribution for detection probability is not influenced by data from the regular snorkeling and single-pass electrofishing index sites. Ideally, we could have sampled from the full range of detection probability hyper-distributions of detection probability in the second estimation phase. This latter approach, which integrates over the full uncertainty in detection probability hyper-parameters, increases computational time by two to three orders of magnitude. During the initial model development of a similar HBM for the Cheakamus River, Korman et al. (2010b) compared uncertainty in juvenile steelhead standing stock estimates based on the median vs. fully integrated two-phased estimation approaches and found the increase in uncertainty under the latter approach was relatively modest (a few %). Based on their results, we adopted the more computationally efficient median approach. Korman et al. (2010b) also used computer simulations to evaluate the extent of bias in standing stock estimates and hyper-parameters generated from the Cheakamus River HBM and found that bias to be negligible in all cases. To describe the precision of the standing stock estimates, throughout the report we use percent relative error, which we computed as the average half credible interval (upper 95% credible limit minus the lower credible limit divided by two and then divided by the mean and expressed as a percentage; Krebs 1999).

2.8 Habitat-based predictors of parr abundance

We utilized direct multiple linear regression (Tabachnick and Fidell 2001) to evaluate whether habitat-based variables were useful predictors of steelhead parr abundance at the site level. Parr abundance at each site was standardized as a density (number per km), included both

age-1+ and age-2+ fish, and was computed as an average across all years of available data. Sites were included in the analysis only if they had been sampled in at least four years. Site-level habitat variables considered for the analysis are described in Section 2.2. Two additional habitat variables were derived from a GIS database: distance from the mouth of the stream, and proximate stream gradient using methods described by Parken et al. (2002) and Williams et al. (1999). For the latter variable, average stream gradient was estimated for 1 km long sections within each stream using GIS streambank elevation data, and individual sites were assigned the gradient estimate for the section in which they occurred. If necessary, independent variables were natural log-transformed to meet requirements for multivariate normality and linearity (Tabachnick and Fidell 2001), as was the dependent variable.

To identify multicollinearity, and to increase the power of the regression analysis to evaluate individual predictors, we examined a Pearson product-moment correlation matrix and set a target level for bivariate correlations among predictors of approximately 0.5 or less. Prior to regression analysis, single predictors were selected for inclusion in the model from among groups of redundant and/or highly correlated variables. For habitat variables that were correlated with one another, priority for inclusion in the model was given to those with logical potential for a causal relationship with steelhead parr abundance, and a straightforward and accurate means of measurement in the field. Habitat variables included in the analysis were D90, mean depth (DMEAN), percentage of fines (< 1 mm) in the substrate (FINESUB), percentage of the site surface area containing turbulence cover (lnTURB), total area of wood debris (LWD), stream gradient (GRADIENT), and distance from the stream mouth (DISTANCE). Individual sites were also placed in one of seven stream categories (STREAM), and one of five habitat type categories (HABTYPE; two tributary types and three mainstem types, see Section 2.2), through the use of two dummy-coded categorical variables. Squared semi-partial correlations (sr_i^2) were used to assess the unique contribution of statistically-significant predictors to the simple multiple linear regression.

With respect to designing population abundance monitoring studies, another important question is whether abundance is more variable in ‘marginal’ relative to ‘core’ rearing habitats. We assessed this using a second multiple linear regression model, which included the coefficient of variation (CV) for parr density at each site as the dependent variable, and the same independent variables described above. Sites were included in this regression analysis only if they had been sampled in four or more years, and parr density was greater than zero in at least two of those years.

Lastly, we investigated potential negative effects of interference competition by Chinook salmon fry on steelhead parr and fry in the study area, by computing correlations between the two species in the time series of annual standing stock estimates for the years 2001-2008 (years for which Chinook fry standing stock estimates are available; Decker et al. in prep.).

2.9 Stock-recruitment analyses

2.9.1 Data

Stock-recruitment analyses were based on age-1+ steelhead parr abundance data for 2001-2012, paired with brood spawner abundance for two individual tributary populations (Deadman, Bonaparte), and for two aggregate stocks. The first, the Nicola aggregate stock³, includes age-1+ parr production from the Nicola River, tributaries Spius Creek and the Coldwater River, and reach T3 of the Thompson River mainstem. The otolith microchemistry analysis of Hagen et al. (2012) indicated that age-1+ parr of the Nicola aggregate are primarily of anadromous maternal origin (steelhead mothers), while parr of the Deadman and Bonaparte stocks are of mixed anadromous and resident maternal origin. Anadromous maternal origin of sampled *O. mykiss* parr within Thompson reach T3 (Figure 1), along with a sharp increase in age-1+ parr density downstream of the Nicola River confluence, suggests that parr rearing within this reach are primarily of Nicola origin and should be included within the Nicola aggregate⁴. The Thompson aggregate stock is simply the total estimated abundance of *O. mykiss* within the study area.

Spawner abundance data for Deadman and Bonaparte rivers, since 1999 and 2002, respectively, are based on electronic counts of migrating spawners over resistivity counters (McCubbing 2002; McCubbing 2009; McCubbing and Bison 2009). In years when resistivity counters operate continuously and without significant interruption (as has been the case in most years to date), precision of abundance estimates are high in comparison to more traditional abundance estimation surveys. In the Nicola basin, spawning population abundance is estimated by combining periodic spawner counts with telemetry-based estimates of residency time, observer efficiency, spatial distribution, and mortality (Bison 2006). The process model accounts for the arrival and departure of fishing into and out-of a survey area and predicts the number of spawners that will be observed over the course of the spawning season (Hilborn et al. 1999). Precision of abundance estimates is more typical of traditional estimation surveys, due mainly to the uncertainty associated with the observer efficiency parameter. Median coefficient of variation is 40% for estimates of Nicola spawner abundance from 1999 to the present.

2.9.2 Stock-recruitment models

To estimate the average relationship between spawner and parr abundance, conventional Ricker and Beverton-Holt models (Ricker 1975) were used. Maximum recruitment was estimated using both approaches. Estimates of population productivity (recruits per spawner at low stock sizes) were derived using only the Ricker model. Estimates of productivity based on

³ The present design of the escapement monitoring program does not allow for discrete estimates for spawning populations in the Nicola River its two sub-tributaries, Spius Creek and Coldwater River; or for the Deadman River and its sub-tributary, Criss Creek.

⁴ Further analysis of tributary residence history for Thompson River parr is pending (see Hagen et al. 2012).

the Beverton-Holt model were expected to be biased high given the degree of statistical contrast and measurement error contained in our data.⁵

We use a Ricker model of the form:

$$R = aSe^{-bS}e^{\epsilon}$$

where R is recruitment (i.e. age-1+ parr abundance) resulting from S , the spawning stock, a is the average number of recruits produced at low spawner abundance (referred to in this report as R/S_{max}), b relates to the rate of decrease in productivity as the spawning stock increases, and e^{ϵ} indicates that the residual errors between predictions of R and the observed production of recruits are expected to be log-normal. Maximum recruitment (R_{max}) of the dome-shaped Ricker stock-recruitment curve is given by:

$$R_{max} = \frac{a}{b}e^{-1}$$

The Beverton-Holt stock-recruitment model is asymptotic in nature, with the maximum recruitment asymptote reflecting the carrying capacity of the environment:

$$R = \frac{aS}{b+S}e^{\epsilon}$$

R , S , and e^{ϵ} are recruitment, spawning stock size, and lognormal expectation for residual errors, a is the maximum number of recruits produced, and b is the spawning stock needed to produce recruitment equal to half the maximum.

Maximum likelihood estimates of Ricker and Beverton-Holt stock-recruitment parameters were estimated as the values that maximized the lognormal probability of the observed recruitment estimates across all sampling years, given the observed estimates of brood spawner abundance. Maximum likelihood estimates were computed in Excel using the Solver non-linear iterative search routine.

⁵ For the purpose of estimating S_{msy} , fisheries scientists prefer the Ricker function even when stock-recruitment curves are not dome-shaped, because it can provide more accurate or more conservative estimates of stock productivity, which leads to better policy advice given the disproportionately high socio-economic costs of overfishing compared to underfishing that is typical of most fisheries (Walters and Martell 2005). Cramer et al. (2004) generated Beverton-Holt and Ricker estimates of R/S_{max} for seven steelhead populations in the mid-Columbia River based on empirical adult-adult stock-recruitment data. For these stocks, Beverton-Holt estimates of R/S_{max} were highly variable, and in some cases unrealistically or extremely high. This is to be expected when significant uncertainty exists in estimates of spawning stock, which has the effect of spreading the stock-recruitment data out along the x-axis and making the stock appear more productive than it is in reality (Hilborn and Walters 1992). For this reason, we take in to consideration only the Ricker R/S_{max} when discussing stock productivity or potential reference points that are conditional on productivity.

Estimates of S_{msy} , the adult stock size associated with maximum sustained yield (MSY), requires information about the elevation of the stock-recruitment curve above the line of replacement (1:1 recruitment:spawner ratio), so spawning stock size and recruitment must be expressed in the same units. We developed stock-specific scaling parameters by estimating mean parr-adult survival. Age-1+ parr cohorts from 2001-2008 were intercepted in commercial fisheries in the fall of 2004-2011, and spawned in the spring of 2005-2012, respectively. Adult steelhead fishing mortality rate estimates for fall 2004-2011 (Bison 2007; Bison 2009) were used to expand spawning escapement estimates for spring 2005-2012. For each stock, we estimated age-1+ parr-adult survivals for individual cohorts by dividing the expanded escapement estimate by the corresponding (4 years earlier) age-1+ parr standing stock. Survival estimates were averaged across cohorts for each stock to derive the scaling parameters used to express recruitment on the equivalent scale as the spawning stock size. With the exceptions of the Nicola aggregate and Thompson aggregate⁶, the parr-adult survival estimates will be biased high because parr production in the Thompson River mainstem also contributes to subsequent tributary escapements. This does not affect the shape of the derived stock-recruitment curve, but it will result in underestimates of R_{max} and S_{msy} , at least for the Deadman and Bonaparte stocks, because parr-adult survival influences the position of the stock-recruitment curve relative to the line of replacement (see Figure 7).

For the Beverton-Holt function, estimates of S_{msy} , for each stock or stock aggregate were:

$$S_{msy} = a \sqrt{\frac{b}{a}} - b$$

In the case of the Ricker stock-recruitment curve, we made use of an adaptation (CTC 1999) to Hilborn's (1985) approximation to Ricker's (1975) iterative procedure:

$$S_{msy} \cong \frac{\ln a + \frac{\sigma_\varepsilon^2}{2}}{b} \left[0.5 - 0.07 \left(\ln a + \frac{\sigma_\varepsilon^2}{2} \right) \right]$$

The term $\frac{\sigma_\varepsilon^2}{2}$ is a correction for process error (but not measurement error) in the stock recruitment relationship, calculated from the following equations:

$$\sigma_\varepsilon^2 = \sigma_{res}^2 - \sigma_{meas}^2 \quad \sigma_{meas}^2 = \frac{\sum_i^n cv^2(R_i) + cv^2(S_i)}{n}$$

⁶ Survival estimates for these aggregate stocks may also be biased high if significant numbers of Thompson steelhead parr also rear downstream in the Fraser River.

where σ_{res}^2 and σ_{meas}^2 are the variance of residuals from the stock-recruitment relationship and the total sampling variance, respectively, and $cv^2(R_i)$ and $cv^2(S_i)$ are the squared coefficients of variation for the estimates of recruitment and spawning stock size, respectively, in year i .

2.10 Evaluation of habitat capability models using empirical data

In the absence of empirical stock-recruitment data, estimates of habitat capability for the Thompson River and other large interior river basins in British Columbia have relied on deterministic habitat capability models (e.g., Tautz et al. 2002; Bocking et al. 2005), steelhead smolt data from other streams (primarily the Keogh River), and Atlantic salmon data from streams in Eastern Canada. Riley et al. (1998) used a generalized habitat capability model to estimate steelhead carrying capacity in lower Thompson River streams. Key inputs in their study were observed empirical relationships between maximum juvenile steelhead densities in optimal habitat, fish size, and total alkalinity (Ptolemy 1993), and model-derived estimates of useable area, mean smolt age, and fry-to-smolt survival (determined by smolt age). Other modeling approaches to estimating steelhead smolt carrying capacity in BC streams have included applying estimates of Keogh River production at carrying capacity (per kilometer, per m^2 of stream, or per m^2 of useable stream area; see Tautz et al. 1992), or Symons' (1979) empirical estimates of maximum production for Atlantic salmon per m^2 of stream, which is based primarily on mean smolt age (Tautz et al. 1992).

We compared our empirical carrying capacity estimates for individual streams within the lower Thompson River to predictions from the habitat capability models described above, as a means of evaluating the accuracy of the latter. In addition, we employed simple correlation analyses to investigate whether the key parameters (estimated useable area, and assumed mean smolt age and fry-to-smolt survival) used in a previous habitat capability model for lower Thompson River streams (Riley et al. 1998) were correlated with our empirical estimates of parr abundance.

To allow for a direct comparison with habitat capability model predictions, we developed smolt carrying capacity estimates using R_{max} values provided by fitting the Beverton-Holt function to our data (see above). We converted our estimates of parr yield per km at R_{max} to smolt yield based on estimates of parr-smolt survival from other studies. Tautz et al. (1992) found that a mean annual survival of 48.8% per year was a good approximation for juvenile steelhead in the Keogh River; whereas a survival rate of 40% for age-1+ parr to age-2+ smolts can be derived from Symons' (1979) study of Atlantic salmon smolts. Approximately 90% of Thompson River steelhead smolt at age-2+. Given that the Thompson River is further from the ocean than the Keogh River, and that parts of the basin experience ice formation during the winter, we used Symons' estimate of 40% parr-smolt survival because it was more conservative.

Escapement data cannot be reliably segregated for streams within the Nicola basin. Therefore, to generate estimates of smolt yield per km at R_{max} for these streams, we assumed that each stream's proportional contribution of age-1+ parr to the total standing stock for Nicola basin, averaged across years, was representative of the relative contribution of each to total smolt yield (e.g., if the Coldwater River is 80 km long and contributes, on average, 35% of the age-1+ parr standing stock, and the total smolt yield for the Nicola basin at R_{max} is 100,000 smolts, then smolt yield at R_{max} for the Coldwater would be 438 smolts/km). Estimated smolt yield was averaged for the Deadman River and its tributary, Criss Creek, because these streams were not treated separately by Riley et al. (1998).

3.0 RESULTS

3.1 Sampling effort

During 2001-2012, low stream flows and turbidity generally provided good to excellent survey conditions, and juvenile steelhead abundance was sampled at 151 to 159 sites each year (2005 and 2010 were exceptions; see paragraphs below and Table 2). Overall, about 80% of sites were sampled by night snorkeling, with the remainder sampled by single-pass electrofishing (Table 2). Snorkeling sites in run habitat strata in the Thompson River tributaries ranged in length from 10-138 m (averages: 20-67 m; Table 2), while single-pass electrofishing sites in riffles ranged from 10-31 m in length (averages: 13-21 m; Table 2). The total length sampled each year equated to approximately 5,400 linear m of stream channel, or a sampling intensity of about 1.1%. Sampling occurred mainly in October during which time water temperatures ranged from 4°C to 10°C in upper Spius and Criss Creeks, from 5°C to 12°C in the Bonaparte and Deadman rivers and lower Spius Creek, from 4°C to 12°C in the Coldwater River, and from 8°C to 14°C in the Nicola and Thompson rivers.

Due to above-average rainfall in 2005, stream flows in Spius Creek and Coldwater River remained well above 1 m³/s for most of October. As a result we were unable to use electrofishing to sample shallow riffles in these streams, and these strata went unsampled (Table 2). In 2005 we were also unable to conduct snorkeling counts in the Bonaparte River due to high streamflows and turbidity. During 2010, high water levels in Nicola Lake and wave action at the lake's outlet resulted in moderate turbidity in the Nicola River downstream to the Thompson River confluence. As a result all our strata in the Nicola River that are sampled by night snorkeling (N1 runs and riffles, N2 runs) could not be sampled in 2010 (Table 2). We were able to sample riffles in reach 2 of the Nicola River (N2 riffles; Table 2) because this stratum is sampled by electrofishing, which was not unduly effected by the higher than normal turbidity levels.

To generate total standing stock estimates for the Thompson River system as a whole in 2005 and 2010, it was necessary to approximate standing stock estimates for these unsampled strata. We assessed the linear regression relationships between annual fish standing stocks in these strata (or streams) versus standing stocks in nearby strata (or streams) in years where data were available for both, and used the regression equation with the highest r^2 value to approximate the standing stock for the strata (or stream) for the missing year. Upper and lower 95% credible intervals and CV values for approximated standing stocks for unsampled strata (or streams) were obtained by simply averaging the percent relative error in standing stock for these same strata (or streams) for years when sampling occurred (Table 3).

Table 3. Summary of parameter values and statistics for linear regression predictions of steelhead parr standing stocks (N) in unsampled streams or habitat strata based on parr standing stocks in surrogate streams or strata. Selection of surrogate streams or strata was based on which had the highest correlation in annual parr standing stocks to those in the unsampled streams or strata in years with no missing data.

Age class	Year	Surrogate stream or strata	Unsampled stream or strata	N (surrogate stream)	Predicted N for unsampled stream or strata	Percent relative error for N for unsampled stream or strata ¹	Regression slope (b)	Regression intercept (a)	r^2
age-1+	2005	L. Spius runs	L. Spius riffles	11,334	23,796	46%	0.89	13765	0.2
age-1+	2005	Coldwater runs	Coldwater riffles	21,744	17,976	48%	0.75	1755	0.3
age-1+	2005	Thompson (all)	Bonaparte (all)	32,056	21,167	31%	0.34	10345	0.2
age-1+	2010	Spius (all)	L. Nicola (all) + U. Nicola runs	38,285	31,027	27%	0.85	-1615	0.6
age-2+	2005	L. Spius runs	L. Spius riffles	2,144	2,017	76%	0.89	103	0.4
age-2+	2005	Coldwater runs	Coldwater riffles	4,920	2,560	65%	0.47	226	0.4
age-2+	2005	Deadman (all)	Bonaparte (all)	1,670	4,208	35%	1.76	1268	0.6
age-2+	2010	Spius (all)	L. Nicola (all) + U. Nicola runs	7,772	10,283	35%	1.47	-1133	0.6

¹Average of values from other years.

3.2 Length-at-age

During 2001-2012 readable scale samples were obtained for a total of 663 steelhead that ranged in size from 42 mm to 275 mm fork length and in age from 0+ to 3+ (Appendix 1). In general, plotted histograms for lengths recorded during snorkeler counts and electrofishing showed clear length-frequency ‘cut-offs’ between age-0+ fry and age-1+ parr, which were in good agreement with the cut-offs suggested by the scale age data. However, in many cases, length-frequency histograms did not suggest clear length cut-offs between age-1+ and age-2+ parr. To estimate length cut-offs for older age classes we relied mainly on the scale age data (Appendix 1). The mean length of age-1+ parr varied considerably among the 12 study reaches (Figure 2), and trended towards larger body size with increasing stream order. Average age-1+ parr were largest in the Thompson River (129-130 mm), somewhat smaller in the primary tributaries (Nicola, Bonaparte and Deadman; 112-125 mm) and smallest in the secondary tributaries (Coldwater, Spius and Criss; 100-106 mm). This pattern was similar for age-2+ parr as well (Figure 2). The length frequency and scale data suggested that, for individual reaches, length-age relationships varied little (± 10 mm) among years.

3.3 Mark-recapture estimates of snorkeling detection probability

Results of the Hagen et al. (2010) mark-recapture study of snorkeling capture probability are paraphrased below. During 2003-2005 a total of 663 steelhead parr were marked across the 51 mark-recapture experiments in seven streams (Table 4). The number of parr captured by snorkelers and marked at each site (all size classes pooled) ranged from 3 to 27, and averaged 13. The mean length of marked parr varied little among the six tributary streams to the Thompson River but was considerably greater in the Thompson River mainstem (Table 4). A total of 433 marked fish were resighted during the second sampling events of these experiments. Aggregated across experiments, the ratio of marks resighted to marks applied was 0.65. Detection probabilities at individual sites were consistently high and moderately precise (Figure 3), with the average coefficient of variation (CV) of detection probability estimated to be 0.24. Low detection probabilities at two sites in the Nicola River (0.12 and 0.15; Figure 3) were likely caused by atypically low underwater visibility (≈ 2 m compared to 2.5-10.4 m at other sites), which was the result of a heavy rainstorm that occurred during the 24-hour interval between the marking and recapture events.

The assumption that populations within sample sites could be treated as effectively closed for the 24-hour period between marking and recapture events was strongly supported. Of the 433 marked parr that were re-sighted by snorkelers across all sites, only 15 parr had moved beyond the boundaries of the original marking area into one of the adjacent sections (5 upstream and 10 downstream). Given that some marked parr potentially moved beyond the adjacent sections that were sampled, the minimum emigration rate of marked parr from the site was 3.5%.

The most parsimonious model of snorkeling detection probability included the effects of two factors: fish size and cross-sectional area of the sampling site. Estimated across all study

streams, the 100-170 mm fork length class had a higher mean detection probability (0.71) than both the 80-100 mm (0.53) and the >170 mm (0.38) classes, while cross-sectional area of the sampling site had a negative effect on detection probability. As an indication of the magnitude of the effect, a four-fold increase in the cross-sectional area of a sampling site would correspond to a predicted decrease in detection probability from 0.60 to 0.41 for parr in the middle size class (100-170 mm)⁷.

⁷ As described in Section 2.7, the HBM incorporated two additional levels of stratification for three fish size classes and two stream size classes to account for the effects of these factors on snorkeling efficiency.

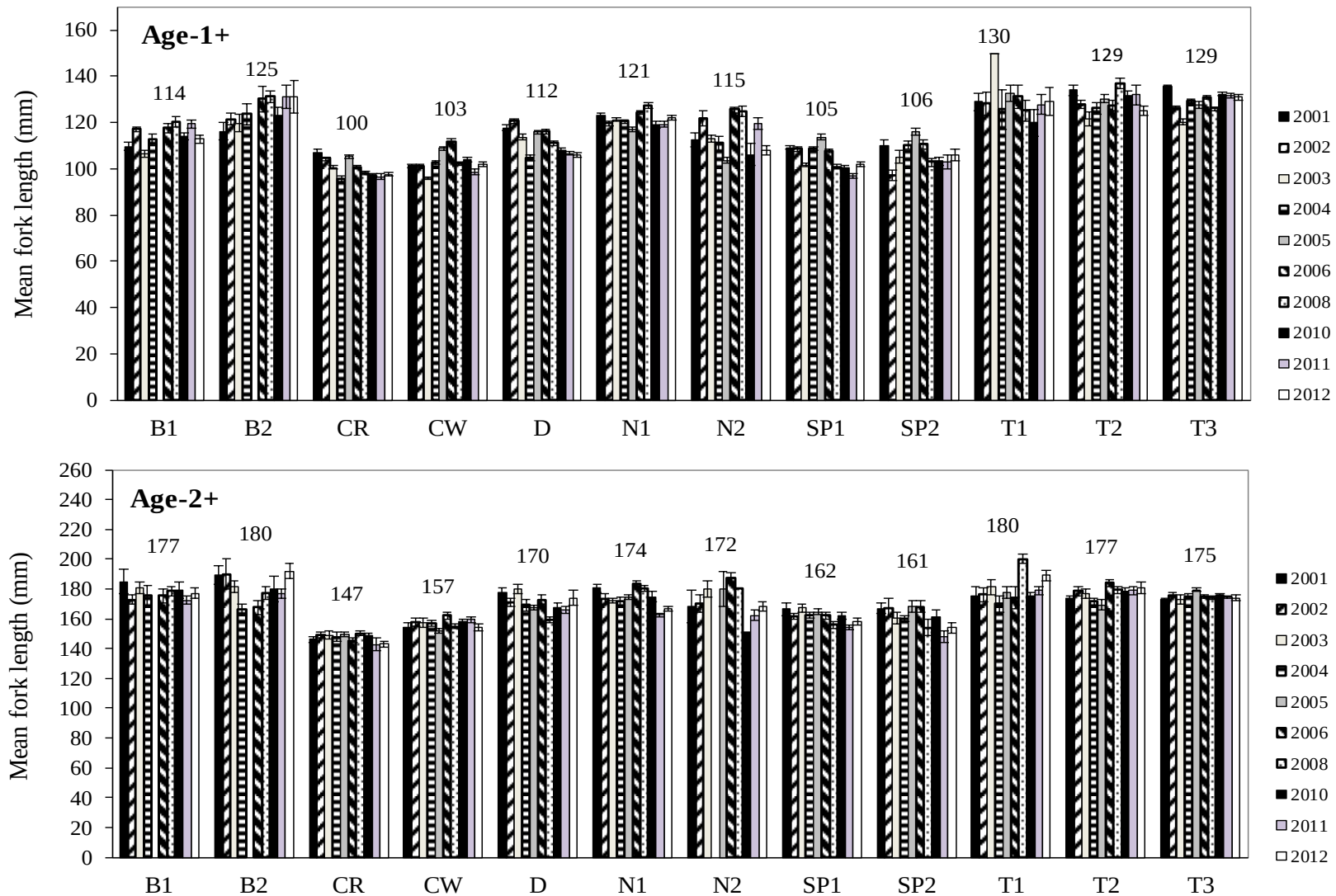


Figure 2. Mean fork lengths of age-1+ and age-2+ steelhead parr in 12 study reaches in the Thompson River basin during 2001-2012. Error bars represent ± 1 standard error of the mean. Numbers above bars are means across years.

Table 4. Summary statistics by stream for steelhead parr collected during mark-recapture experiments in the Thompson River basin, 2003-2005 (adapted from Hagen et al. 2010).

Stream	Mark-recapture sites (all years)	Mean site length (m)	Mean site depth (m)	Total fish marked			Mean detection probability	Mean length marked fish (mm)
				80-100 mm	100-170 mm	>170 mm		
Criss	5	30	0.51	19	54	2	0.79	116
Deadman	5	41	0.59	8	57	1	0.79	119
Coldwater	9	41	0.57	41	69	0	0.63	109
Spilus	11	33	0.53	28	123	5	0.7	120
Bonaparte	3	68	0.7	4	9	0	0.69	117
Nicola	9	70	0.82	25	104	2	0.57	119
Thompson	9	121	1.42	4	78	30	0.54	152

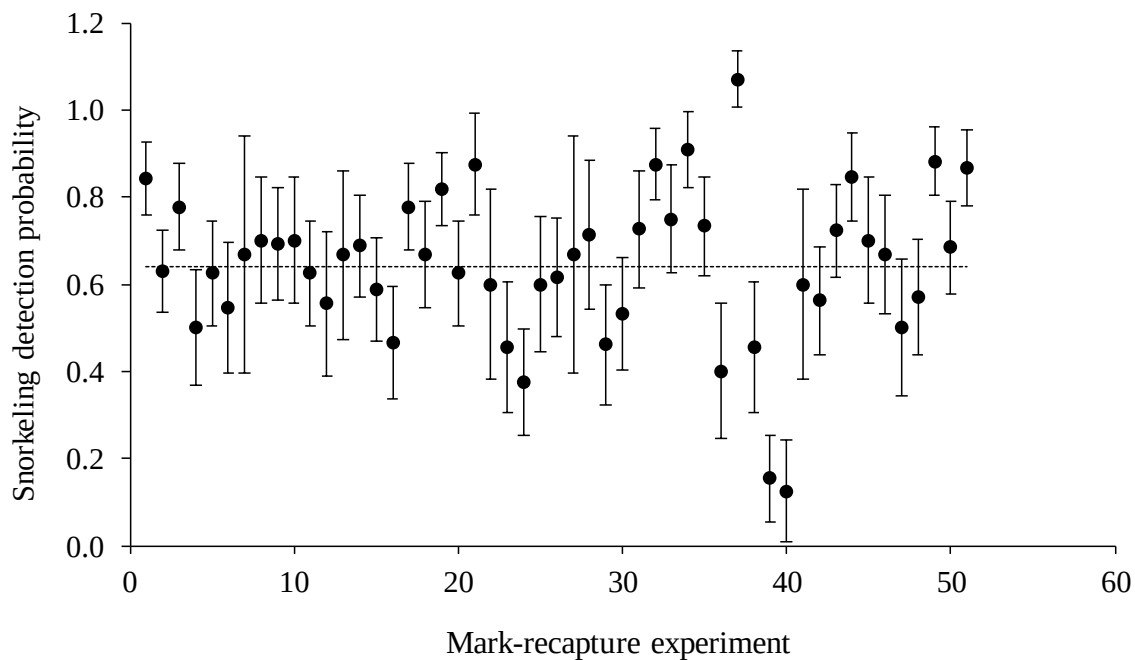


Figure 3. Most likely estimates of snorkeling detection probability for steelhead parr at 51 sites in the lower Thompson River basin based on mark-recapture experiments (adapted from Hagen et al. 2010). Error bars denote the standard errors of the estimates; the dashed line represents the average detection probability across all sites.

3.4 Depletion estimates of capture probability for single-pass electrofishing

During 2001-2005, three-pass removal estimates were obtained at 11 sites in shallow tributary riffle strata where single-pass electrofishing was used as the sampling method (Table 2). Single-pass electrofishing catches were highly correlated with the three-pass removal estimates, explaining 92% and 96% of the variation in the latter among sites for steelhead parr and fry, respectively (Figure 4). Estimated capture probabilities for a single electrofishing pass were very high, averaging 0.83 and 0.71 for steelhead parr (age-1+ and 2+ fish pooled) and fry (age-0+), respectively, and relatively precise (CV = 0.20 and 0.11, respectively).

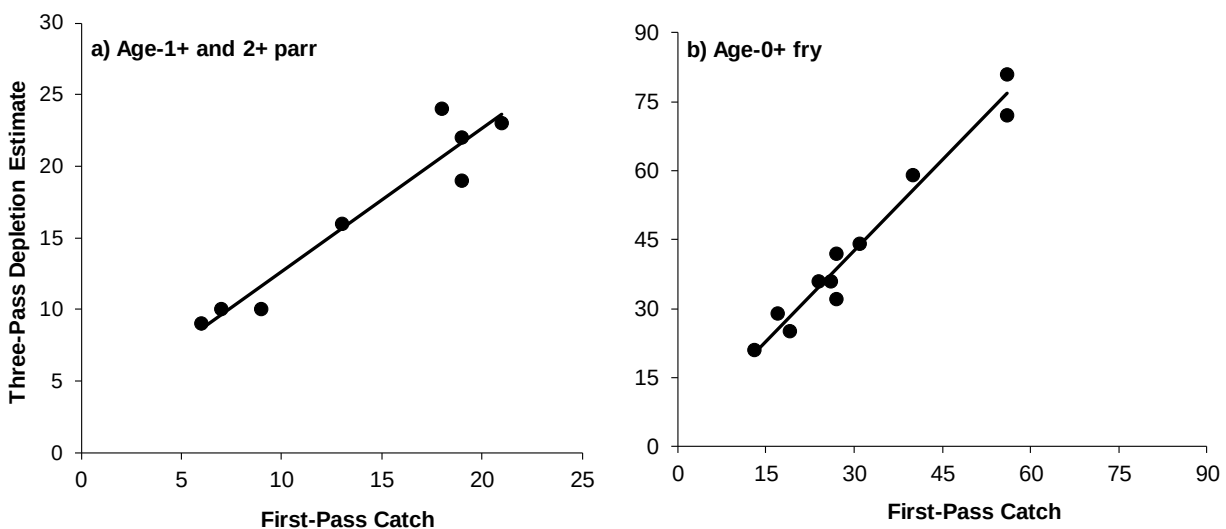


Figure 4. Relationships of three-pass electrofishing depletion estimates to first-pass catches of a) age-1+ steelhead parr and b) age-0+ fry in shallow riffle sites in small tributary reaches in the lower Thompson River basin.

3.5 Juvenile steelhead standing stocks

3.5.1 Steelhead parr

During the hierarchical Bayesian estimation of juvenile *O. mykiss* population abundance, some strata were aggregated to improve the population estimation results (25 strata were delineated in earlier assessments, see Table 2). Among the resulting 19 reach/habitat type strata (Table 5), parr density (age-1+ and age-2+ parr combined) when averaged across years varied 18-fold. Variation in parr density among streams and reaches was high, and exhibited a similar pattern among years (Figure 5a, 5b). Among streams, the two smallest and highest gradient tributaries in the study area, Spius and Criss creeks, supported the highest parr densities in all years (Figure 5b). The Nicola River, Coldwater River, and the Deadman River had intermediate parr densities, while the Thompson and Bonaparte rivers had the lowest parr densities, averaged

across their entire lengths. However, parr densities in the lowermost canyon reach of the Thompson River (T3) were among the highest in the study area (Figure 5a). For individual streams that were stratified into two or more reaches, there was a consistent pattern of higher parr density in the downstream reach (Figure 5a). In contrast to the high spatial variation in parr density, among-year variation in parr density within individual streams and reaches was relatively low (Figure 5a, 5b).

During 2001-2012, age-1+ parr standing stocks for the study area as a whole averaged 211,591 fish, and varied only moderately among years (158,877-247,934; Table 6). Age-2+ abundance averaged 53,494 fish and exhibited greater fluctuations during the 2001-2012 study period (34,748-95,873 parr; Table 7). Estimates of parr standing stocks for the study area as a whole were relatively precise, with percent relative error ranging from $\pm 11\%$ to $\pm 17\%$ among years for age-1+ parr (Table 6), and from $\pm 13\%$ to $\pm 25\%$ among years for age-2+ parr (Table 7). Average precision of annual age-1+ parr standing stock estimates for individual streams, estimated among years, ranged from $\pm 26\%$ (Coldwater River) to $\pm 33\%$ (Nicola River, Criss Creek). Average precision of the age-2+ parr standing stock estimates, calculated in the same way, ranged from $\pm 34\%$ (Coldwater River) to $\pm 48\%$ (Criss Creek).

Correlations among annual age-1+ parr standing stocks were not strongly evident. Pairs of tributary streams within the same basin (Nicola, Deadman) were correlated but not strongly, with the exception being the adjacent streams Nicola River and lower Spius Creek, which had one of only two pairwise comparisons of $r > 0.5$ (Table 8). Parr abundance in the Coldwater River was only weakly correlated with that in Nicola River or Spius Creek, despite the close proximity of these streams in the Nicola Basin. Interestingly, the only other moderately strong correlation was a negative correlation between age-1+ standing stocks in the Deadman system and for the Thompson system as a whole.

On average, age-1+ parr represented 80% of the combined total standing stock of age-1+ and age-2+ for the study area during 2001-2012 (range: 67%-86%). The proportion of age-1+ parr was lowest in the Thompson River mainstem (2001-2012 mean: 54%; Tables 6 and 7). Among tributaries the average proportion of age-1+ parr ranged from 83% in the Nicola and Bonaparte rivers to 92% in the Deadman River.

Table 5. Summary of mean parr (age-1+ and age-2+ fish combined) densities across years (2001-2012) for 19 habitat strata in the lower Thompson River basin. Minimum and maximum values for mean density among years are also shown.

Stream	Reach	Habitat type	Parr/km (2001-2012)		
			Mean	Minimum	Maximum
Bonaparte	-	riffle	127	36	214
	-	run	314	135	415
Criss	-	riffle	1,320	737	2,176
	-	run	2,315	1,536	4,015
Coldwater	-	riffle	413	215	635
	-	run	800	572	1,111
Deadman	-	riffle	273	96	620
	-	run	917	587	1,145
Nicola	N1	riffle	694	401	1,303
	N1	run	919	560	1,431
Nicola	N2	riffle	165	46	244
	N2	run	301	140	667
Spius	SP1	riffle	1,358	943	2,460
	SP1	run	1,553	1,112	2,387
Spius	SP2	riffle	650	444	818
	SP2	run	688	397	1,181
Thompson	T1	all	125	82	165
	T2	all	310	198	429
	T3	all	1,384	594	2,495

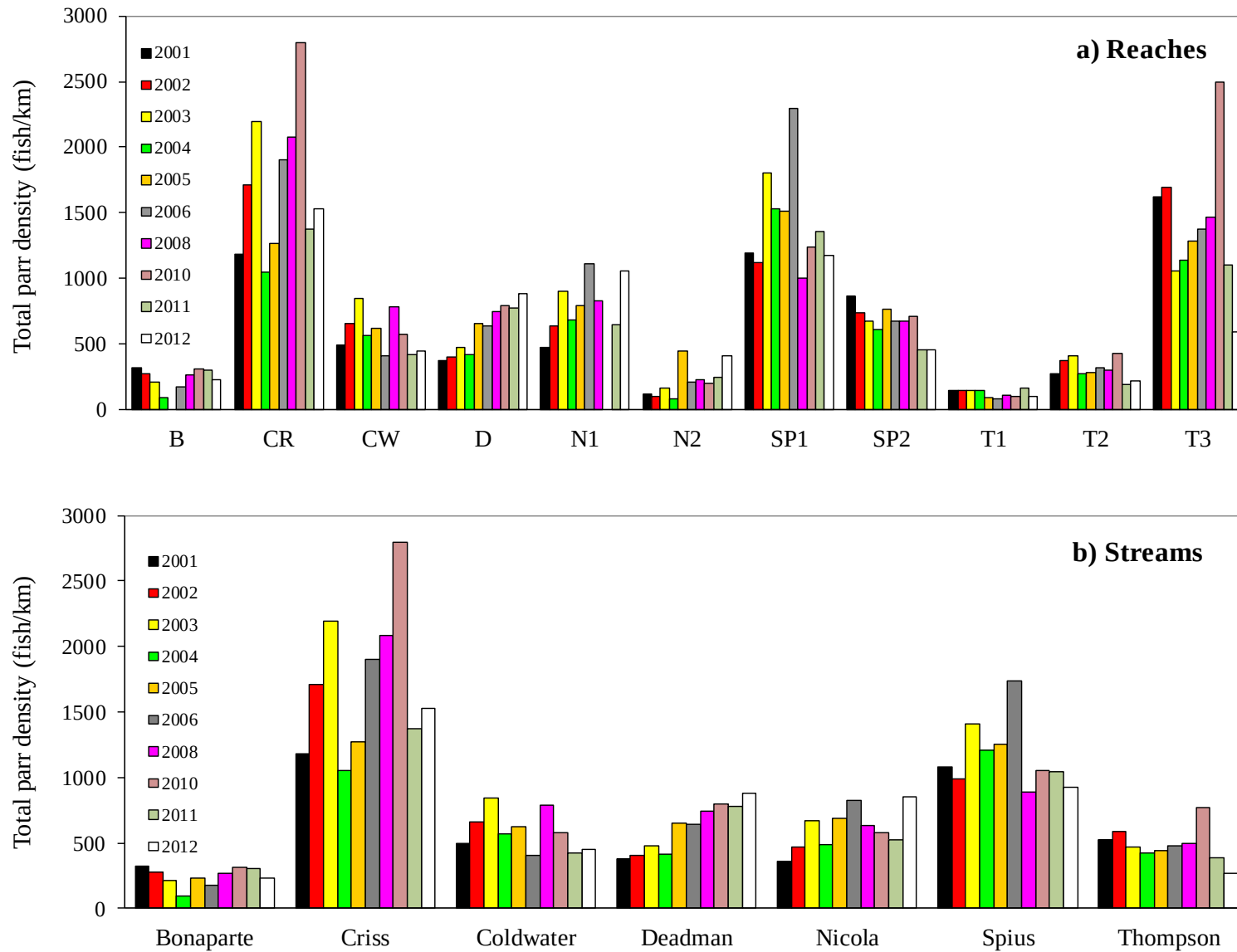


Figure 5. Mean steelhead parr (age-1+ and age-2+ combined) densities (fish/km) by (a) reach and (b) stream in the lower Thompson system during 2001-2012. See Tables 6 and 7 for 95% credible intervals computed separately for age-1+ and age-2+ standing stocks.

Table 6. Estimated age-1+ steelhead parr standing stocks and 95% credible intervals (shown as percent relative errors; see Section 2.7.2) for all study reaches in the Thompson River basin during 2001-2012.

Stream or reach	Standing Stock											Percent relative error										
	2001	2002	2003	2004	2005	2006	2008	2010	2011	2012	mean	2001	2002	2003	2004	2005	2006	2008	2010	2011	2012	
Bonaparte	32,631	28,005	19,173	8,603	ND ¹	17,453	21,139	29,698	20,876	20,145	21,969	26%	29%	28%	32%	ND ¹	29%	34%	32%	37%	39%	
Criss	12,331	19,375	26,691	12,111	12,361	21,867	23,746	30,967	16,579	19,124	19,515	44%	29%	29%	32%	42%	31%	30%	32%	30%	29%	
Coldwater	35,666	46,429	63,257	41,030	41,916 ²	27,805	56,611	36,082	26,949	30,082	40,583	26%	24%	22%	22%	25%	28%	23%	28%	30%	27%	
Deadman	12,193	13,404	16,884	14,488	22,668	21,376	22,912	25,121	24,307	30,483	20,384	35%	29%	30%	30%	30%	28%	29%	27%	29%	33%	
Nicola	23,354	31,310	43,033	32,992	45,978	59,451	44,885	32,691	23,157 ²	41,090	37,794	38%	34%	33%	27%	24%	29%	29%	27%	38%	47%	
Spius	38,656	35,818	51,091	45,218	43,588 ²	61,960	31,447	34,011	34,011	26,952	40,275	41%	32%	26%	20%	29%	30%	26%	28%	26%	31%	
Thomp. (T1)	1,351	1,999	351	1,277	561	1,503	1,437	737	1,515	1,658	1,239	45%	45%	40%	45%	51%	47%	40%	46%	45%	51%	
Thomp. (T2)	5,790	12,509	7,654	6,968	9,841	7,452	4,246	9,194	1,844	7,783	7,328	37%	40%	43%	40%	45%	45%	38%	43%	43%	45%	
Thomp. (T3)	31,047	35,371	19,800	21,091	18,551	25,055	28,810	26,661	9,639	9,815	22,584	38%	35%	35%	32%	45%	42%	22%	32%	30%	41%	
Thomp. (all)	38,188	49,879	27,805	29,336	28,953	34,010	34,493	36,592	12,998	19,256	31,151	31%	28%	26%	25%	33%	33%	18%	25%	22%	30%	
Total	193,019	224,220	247,934	183,778	216,631 ²	243,922	235,233	225,162	158,877 ²	187,132	211,591	15%	13%	13%	11%	13%	14%	11%	12%	13%	17%	

¹ ND indicates no data were collected for a particular reach/stream due to high flows (see Methods)

² Age-1+ parr standing stocks were approximated for missing strata to compute these values (see Methods)

Table 7. Estimated steelhead age-2+ parr standing stocks and 95% credible intervals (shown as percent relative errors; see Section 2.7.2) for all study reaches in the Thompson River basin during 2001-2012.

Stream or reach	Standing Stock											Percent relative error										
	2001	2002	2003	2004	2005	2006	2008	2010	2011	2012	mean	2001	2002	2003	2004	2005	2006	2008	2010	2011	2012	
Bonaparte	2,323	1,951	3,553	1,944	ND ¹	1,867	7,318	4,235	11,468	4,824	4,387	35%	35%	40%	23%	ND ¹	37%	36%	42%	28%	50%	
Criss	2,914	2,681	1,650	1,429	4,020	2,692	3,074	5,115	1,151	590	2,532	42%	42%	55%	45%	43%	46%	57%	51%	48%	55%	
Coldwater	3,630	5,647	3,538	3,927	7,393 ²	4,443	5,479	9,436	6,534	5,340	5,537	30%	32%	36%	23%	34%	41%	40%	34%	33%	42%	
Deadman	1,479	1,269	437	604	993	1,853	4,059	3,548	3,748	1,415	1,941	49%	41%	45%	47%	41%	35%	55%	49%	35%	47%	
Nicola	3,548	3,621	6,689	3,589	5,161	2,070	2,669	10,699 ²	15656	22,425	7,613	30%	31%	36%	32%	28%	38%	40%	57%	32%	36%	
Spius	3,318	2,629	3,666	1,885	5,209 ²	5,429	3,139	7,025	6,672	9,101	4,807	40%	44%	37%	46%	39%	34%	45%	35%	34%	35%	
Thomp. (T1)	4,623	3,995	5,424	4,501	3,080	1,728	2,968	3,402	5,016	2,399	3,714	44%	59%	77%	62%	64%	62%	92%	65%	73%	67%	
Thomp. (T2)	9,031	7,793	14,617	8,146	5,531	10,109	12,171	14,000	8,889	4,259	9,455	40%	51%	52%	57%	56%	51%	67%	56%	69%	53%	
Thomp. (T3)	11,271	8,891	7,887	8,723	14,879	10,924	9,430	38,413	19,173	5,690	13,528	34%	39%	42%	34%	36%	27%	28%	49%	45%	35%	
Thomp. (all)	24,925	20,679	27,928	21,370	23,490	22,761	24,569	55,815	33,078	12,348	26,696	22%	35%	39%	35%	31%	30%	44%	41%	42%	36%	
Total	42,137	38,477	47,461	34,748	50,474 ²	41,115	50,307	95,873 ²	78307	56,043	53,494	13%	18%	22%	22%	19%	18%	24%	25%	19%	19%	

¹ ND indicates no data were collected for a particular reach/stream due to high flows (see Methods)

² Age-2+ parr standing stocks were approximated for missing strata to compute these values (see Methods)

Table 8. Pearson correlation coefficients among stream reaches for age 1+ and age 0+ steelhead standing stocks during 2001-2012.

	Bonaparte	Criss	Coldwater	Deadman	Nicola	Spius	Thompson
Age-1+ parr							
Bonaparte	1.000						
Criss	0.216	1.000					
Coldwater	-0.059	0.307	1.000				
Deadman	-0.097	0.332	-0.362	1.000			
Nicola	-0.408	0.282	0.152	0.306	1.000		
Spius	-0.390	-0.008	0.061	-0.368	0.567	1.000	
Thompson	0.462	0.157	0.325	-0.598	0.033	0.129	1.000
	Criss	Coldwater	Deadman	U. Nicola	L. Spius	U. Spius	
Age-0+ fry							
Criss	1.000						
Coldwater	0.238	1.000					
Deadman	0.423	0.206	1.000				
Upper Nicola	0.287	0.478	-0.239	1.000			
Lower Spius	0.233	0.449	0.820	-0.326	1.000		
Upper Spius	0.457	0.089	0.410	0.145	0.521	1.000	
	Bonaparte	Deadman	Nicola				
Age-0+ fry versus brood spawner abundance							
Deadman	-0.112						
Nicola	0.552						
Thompson	0.626						

3.5.2 Steelhead fry

For tributary riffle strata, where age-0+ *O. mykiss* abundance could be estimated based on single-pass electrofishing, fry densities were more variable among years relative to parr densities (Figure 6). Despite this, differences among reaches in fry density were apparent, with the Deadman River, upper Nicola reach, and lower reach of Spius Creek having the higher densities of fry per km in most years, and Criss Creek, Coldwater River, and upper reach of Spius Creek having lower densities.

During 2001-2012, total fry standing stocks for tributary riffles averaged 426,692 fish, and varied from 294,867 to 577,236 fish (Table 9). Although a consistent trend over time was not evident, it should be noted that the three highest standing stocks were observed in the first three years of the study 2001-2003. Pairwise correlations between annual age-0+ fry standing stocks among tributary reaches were generally positive and stronger for adjacent tributaries (Table 8). Age-0+ fry standing stocks in riffles of the Nicola system and in the Thompson system as a whole exhibited moderately strong correlations ($r > 0.5$) with brood spawner abundance estimates (FLNRO Kamloops data on file), while fry standing stock estimates within the Deadman system did not (Table 8).

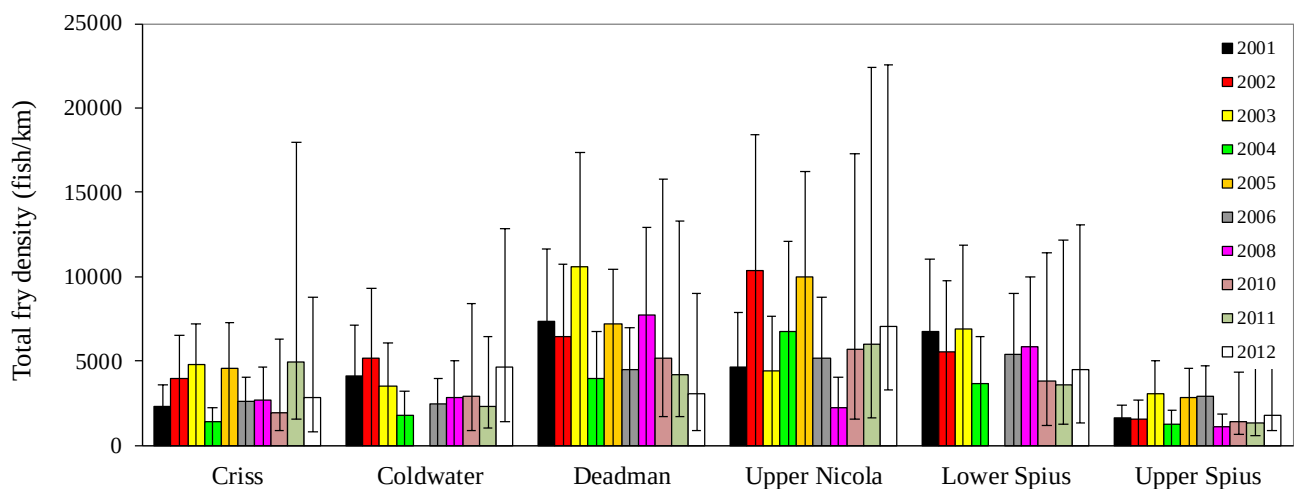


Figure 6. Mean steelhead fry (age-0+) densities (fish/km) in shallow riffle habitat in six tributary reaches in the lower Thompson River basin that were sampled using single-pass electrofishing during 2001-2011. Error bars indicate 95% credible intervals.

Table 9. Estimated age-0+ steelhead fry standing stocks and 95% credible intervals (shown as percent relative errors; see Section 2.7.2) for shallow riffle strata in tributaries where single-pass electrofishing was substituted for snorkeling. Note that totals do not include fry present in habitat strata sampled with snorkeling.

Stream or reach	Standing stock											Percent relative error										
	2001	2002	2003	2004	2005	2006	2008	2010	2011	2012	mean	2001	2002	2003	2004	2005	2006	2008	2010	2011	2012	
Criss	18,328	30,765	37,709	11,055	35,669	20,686	21,212	15,276	38,779	22,006	25,498	79%	47%	63%	52%	76%	90%	48%	74%	74%	56%	
Coldwater	180,189	227,953	153,378	78,136	ND ¹	108,852	124,829	126,228	102,083	205,263	137,706	48%	29%	44%	33%	ND ¹	61%	33%	53%	60%	47%	
Deadman	123,732	107,837	178,416	65,990	120,452	74,807	130,259	86,935	70,843	51,861	106,586	77%	47%	61%	46%	74%	93%	39%	58%	66%	51%	
Upper Nicola	47,806	106,365	45,243	69,252	101,941	52,615	22,695	57,965	61,090	71,792	62,775	54%	34%	48%	37%	50%	70%	42%	54%	70%	75%	
Lower Spius	112,007	91,495	114,425	60,350	ND ¹	89,921	96,766	63,631	58,943	74,537	85,942	64%	32%	52%	34%	ND ¹	66%	43%	55%	69%	52%	
Upper Spius	13,026	12,821	25,174	10,084	22,764	23,368	9,015	11,193	10,735	14,504	15,353	76%	52%	72%	49%	65%	71%	48%	73%	81%	58%	
Total	495,088	577,236	554,345	294,867	-	370,249	404,776	361,228	342,473	439,963	426,692	36%	18%	28%	18%	-	38%	21%	31%	33%	30%	

¹ ND indicates no data were collected for a particular reach/stream due to high flows (see Section 3.0)

3.6 Steelhead parr abundance-habitat relationships

Complete habitat data were available for 146 sites for which four or more years of steelhead parr density estimates were available. The habitat variables as a set were reliable predictors of mean parr abundance ($F = 13.1$; $P < 0.001$), explaining 61.9% of among-site variation in mean parr density (Table 10). In order of their contribution to R^2 , significant individual predictors were distance from the stream mouth (negative effect; Table 10), D90 (positive), mean thalweg depth (positive), stream (see Figure 5), and habitat type. With respect to habitat type, parr densities were higher in runs in the tributaries and cobble bars and deep-fast shorelines in the Thompson River compared to those in tributary riffles and Thompson River embayments. Other variables were not significant predictors in the regression solution (Table 10).

Table 10. Multiple linear regression of A) log-transformed mean parr abundance across individual sampling sites versus habitat variables; and B) coefficient of variation (CV) in parr abundance across sites versus habitat variables. Squared semi-partial correlations (sr_i^2) indicate the unique contribution of statistically significant predictors to the regression. See Section 2.8 for descriptions of habitat variables.

Habitat variable	A) Parr abundance			B) CV _{parr abundance}		
	<i>F</i> -ratio	<i>P</i>	sr_i^2	<i>F</i> -ratio	<i>P</i>	sr_i^2
lnD90	30.8	<0.001	0.0862	20.03	<0.001	0.056
lnDMEAN	9.67	0.002	0.0271	8.06	0.005	0.023
lnFINESUB	0.02	0.892	0.0010			
lnTURB	0.11	0.744	0.0003			
lnLWD	0.37	0.542	0.0010			
DISTANCE	32.0	<0.001	0.0898	1.63	0.203	0.005
STREAM	4.56	0.001	0.0128	3.76	0.003	0.011
HABTYPE	8.80	<0.001	0.0247	12.51	<0.001	0.035
GRADIENT	0.69	0.408	0.0019			
<u>Regression statistics</u>						
<i>n</i>	146			148		
<i>F</i> -ratio	13.1			8.93		
<i>P</i>	<0.001			<0.001		
R^2	0.619			0.443		

To test whether annual variation in parr density was more variable in marginal relative to core rearing habitats within individual streams, we repeated the regression analysis with the coefficient of variation in parr density among years (CV_{parr density}) treated as the dependent variable, and the five variables that were significant predictors of mean parr density in the previous analysis treated as the

independent variables. Based on results of the previous regression analysis, we assumed that marginal sites occurred in tributary riffles and in Thompson River embayments, were located in upper sections of streams further from the mouth, and had relatively small substrates and shallow depths, while core rearing areas occurred in run habitat in the tributaries and in cobble bar and deep/fast shoreline habitat in the Thompson River, were located in lower stream sections, had coarser bed material, and were relatively deep. Data for 148 sites were available for the analysis. The predictors as a set reliably predicted coefficients of variation among sites ($F = 8.93$, $P < 0.001$), and explained 44% of their variation (Table 10). On the whole, the notion that steelhead parr abundance was less variable in core rearing habitats was supported by the analysis. Both habitat type and D90 were highly significant predictors of $CV_{\text{parr density}}$ in the expected direction (Table 10). In contrast, mean depth was a significant predictor of $CV_{\text{parr density}}$, but in the opposite direction (parr density was more variable among years in deeper sites), while distance from the mouth was not a significant predictor.

We found no evidence that among-year variation in steelhead parr and fry abundance was negatively affected by Chinook salmon fry abundance. Annual steelhead 1+ parr standing stocks for the study area as a whole (Table 6) were positively correlated with Chinook fry standing stocks presented in Decker et al. (in prep.) up to 2008 ($r = 0.45$). With respect to steelhead fry, combined standing stocks for all shallow riffle strata sampled by electrofishing (Table 10) were positively correlated with Chinook fry standing stocks in these same strata ($r = 0.87$).

3.7 Stock-recruitment

After reconstructing annual adult recruitment using the estimated exploitation rates of 22%, 15%, 21%, 13%, 7.1%, 11%, and 20% for the 2004-2009 and 2011 fishing seasons, respectively, estimates of average age-1+ parr-to-returning adult survival varied from 0.58% - 1.31% among Thompson River stocks (Table 11). Positive relationships of age-1+ parr recruitment to spawning stock are not evident for the Deadman and Bonaparte populations within the 2001-2012 stock-recruitment data, despite 7.2-fold and 5.3-fold contrasts in brood spawner escapement, respectively (Figures 7a, 7b). Declining production of age-1+ parr at low spawning stock size is most evident within the Nicola aggregate stock (which includes production from reach T3 of the Thompson River – see Section 2.9) over a 5.7-fold contrast in brood spawner abundance (Figure 7c), and to a lesser extent the Thompson aggregate stock over a 4.6-fold contrast in brood spawner abundance (Figure 7d). Presumably, this pattern is less evident in the Thompson aggregate stock because of the influence of the Deadman and Bonaparte stock-recruitment data, in which parr abundance and brood spawner abundance do not appear to be positively related.

Table 11. Summary of maximum likelihood estimates of stock-recruitment parameters for three stocks in the lower Thompson River basin, and for the Thompson aggregate stock as a whole. Stock-recruitment parameters shown are average recruits-per-spawner at low spawning stock size (R/S_{max}), maximum recruits at carrying capacity (R_{max}), and adult stock size associated with maximum sustained yield of recruits (S_{msy}). Descriptions of assumptions used to convert parr standing stock estimates to total smolt yield, and equivalent returning adults are provided in Section 2.9.

Stock	Contrast in brood spawner abundance	Age-1+ parr yield		Smolt yield		Parr-adult survival	Equivalent returning adults		
		R/S_{max}	R_{max}	R/S_{max}	R_{max}		R/S_{max}	R_{max}	S_{msy}
Beverton-Holt									
Deadman	7.2-fold	967	47,911	387	19,164	0.73%	7.0 ¹	348	-
Bonaparte	5.3-fold	538	25,971	215	10,388	1.31%	7.0 ¹	340	-
Nicola aggregate	5.7-fold	979	184,120	392	73,648	0.58%	5.7	1,074	-
Thompson aggregate	4.6-fold	1,142	255,699	457	102,280	0.62%	7.0 ¹	1,574	-
Ricker									
Deadman	"	622	47,243	249	18,897	0.73%	4.5	344	125
Bonaparte	"	394	24,479	158	9,792	1.31%	5.1	320	110
Nicola aggregate	"	451	173,753	180	69,501	0.58%	2.6	1,013	403
Thompson aggregate	"	440	240,652	176	96,261	0.62%	2.7	1,481	621

¹ The R/S_{max} parameter was constrained to values <7.03 when estimating R_{max} using the Beverton Holt model – see text.

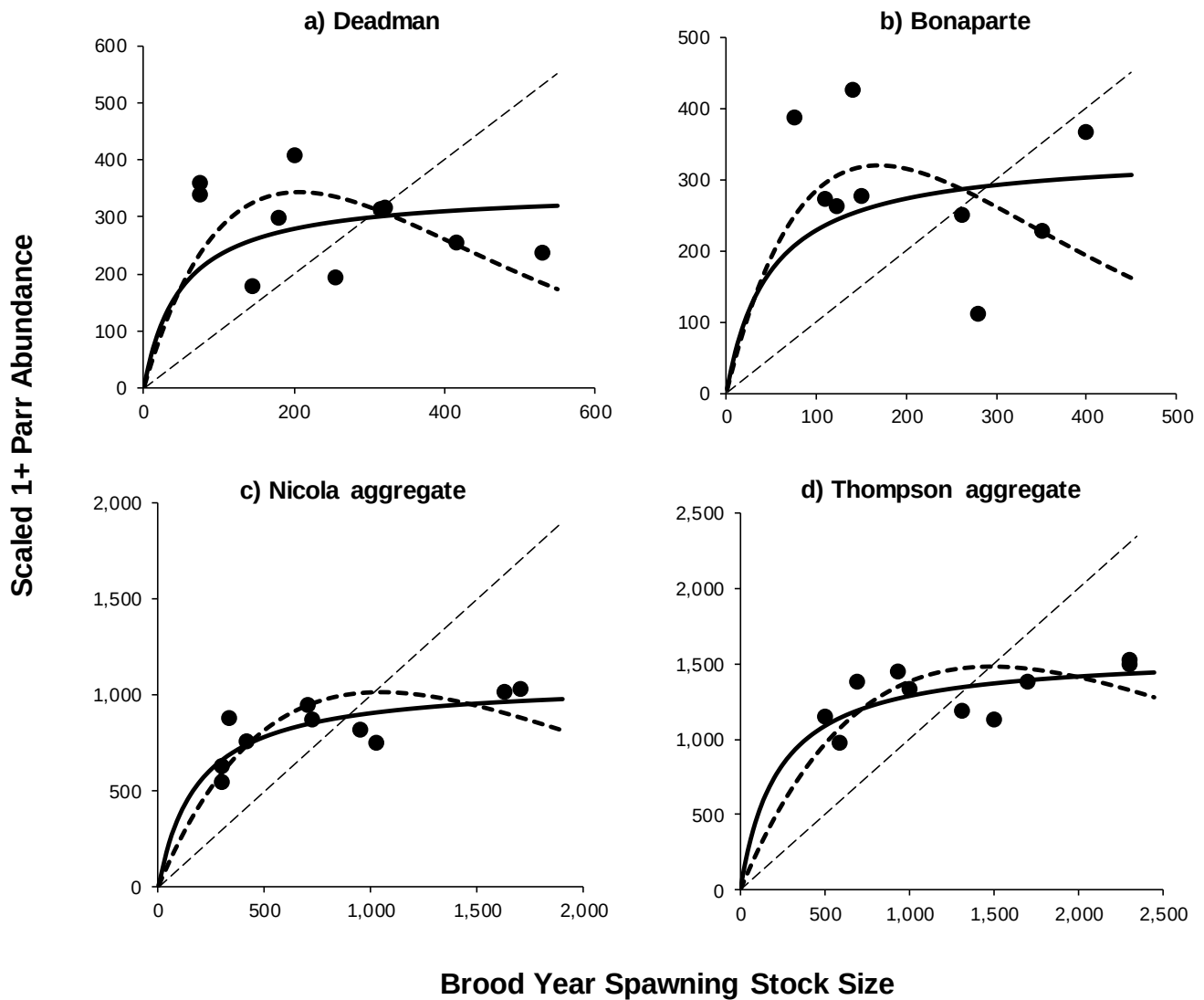


Figure 7. Beverton-Holt (solid line) and Ricker (stippled line) stock-recruitment curves fit to brood spawner escapements and age-1+ steelhead parr standing stock scaled to equivalent adult returns (see Section 2.9) for the a) Deadman, b) Bonaparte, c) Nicola aggregate (including Nicola, Coldwater, Spius, and reach T3 of the Thompson River), and d) Thompson aggregate stocks; the latter represents the combined totals for the entire study area. The dashed diagonal line is the 1:1 replacement line.

For the Deadman and Bonaparte populations, relatively constant parr abundance, and scaled adult recruits to brood spawner ratios of less than 1 (data points to the right of the replacement lines in Figure 7) are evidence of density-dependent survival, and provide approximations of age-1+ parr carrying capacities for these stocks. However, the data do not reveal the steeply ascending portion of the stock-recruitment curves expected for these stocks at very low brood spawner abundance (which is not highly evident for the Thompson aggregate as well), where the number of recruits-per-spawner are highest because of the reduced density-dependent competition and mortality factors. As expected, statistical fits of the Beverton-Holt function to Deadman, Bonaparte, and Thompson aggregate stock-recruitment data resulted in unrealistically high estimates of stock productivity (maximum recruits/spawner: R/S_{max}). Therefore, to estimate carrying capacity R_{max} using the Beverton-Holt model, we constrained R/S_{max} to an upper level of 7.03 (Table 11), which equates to the estimated upper 95% confidence limit for Atlantic salmon (Myers et al. 1999). Estimated Beverton-Holt R_{max} values (returning adults) under current ocean survival conditions were 348, 340, 1,074, and 1,574 fish for the Bonaparte, Deadman, Nicola aggregate, and Thompson aggregate stocks, respectively (Table 11).

Estimates of stock productivity R/S_{max} for the Deadman, Bonaparte, Nicola aggregate, and Thompson aggregate stocks were based the Ricker model and were 4.5, 5.1, 2.6, and 2.7, respectively (Table 11). Ricker stock-recruitment relationships for individual stocks did not suggest the dome-shaped form, except in the case of the Bonaparte River (Figure 7b). Ricker estimates of R_{max} were only slightly lower than the Beverton-Holt estimates (Table 11). Estimates of S_{msy} for the Deadman, Bonaparte, Nicola aggregate, and Thompson aggregate stocks are also based on the Ricker model (due to dependency of S_{msy} on the estimates of productivity) and were 125, 110, 403, and 621, respectively (Table 11). All stock recruitment results expressed in terms of adults are population attributes under the survival conditions (particularly marine survival conditions) experienced over the juvenile monitoring time frame which is brood year 1999 to present.

3.8 Comparison of carrying capacity models

Smolt yield estimates provided by steelhead habitat capability models were generally poor predictors of our empirical estimates of Beverton-Holt smolt yield at carrying capacity (R_{max}) for streams in the lower Thompson River basin and for the Thompson system as a whole (Table 12). Keogh River empirical smolt yield per stream area overestimated our empirical smolt yields from larger streams (Bonaparte, Nicola and Thompson) by 2.0- to 23-fold, but provided reasonable approximations for smaller tributaries (Deadman, Coldwater and Spius). Keogh River empirical smolt yield per useable stream area modestly overestimated smolt yields from larger streams, and underestimated yields from smaller ones. Symons' (1979) empirical biostandard for Atlantic salmon smolt yield per area was the only model that came close to predicting the exceptional smolt yield from Spius Creek, but the model overestimated yields from the other streams by 1.2- to 35-fold. Predictions from

models based on empirical smolt yield per stream length (Riley et. al 1998 and Keogh smolt yield per stream length; Table 13) predicted smolt yield from the Thompson system as a whole reasonably well, but were relatively poor predictors of empirical smolt yields from individual streams (range: 0.2- to 2.8-fold). Similar to the models based on stream area, they tended to overestimate smolt yields from larger streams, and underestimate yields from smaller ones.

Table 12. Comparison of empirical estimates of smolt yield per km at carrying capacity (R_{max}) for lower Thompson River streams (this study) versus predictions from habitat capability models that have been used in other studies of steelhead production in the lower Thompson River basin and in other steelhead streams in British Columbia. Shown in brackets is the magnitude of each model prediction relative to the empirical estimate. Methods used to generate empirical estimates of R_{max} and descriptions of habitat capability models are provided in Section 2.9.4.

Stream	Thompson system empirical carrying capacity estimates	Riley et al. (1998) habitat capability model	Keogh River empirical smolt yield per stream length	Keogh River empirical smolt yield per stream area	Keogh River empirical smolt yield per useable stream area	Symons' (1979) age-2+ smolt yield per stream area
Deadman (including Criss)	363	303 (83%)	230 (63%)	307 (85%)	161 (44%)	479 (132%)
Bonaparte	96	213 (222%)	230 (240%)	401(418%)	85 (89%)	626 (652%)
Nicola	313	537 (172%)	230 (73%)	677 (216%)	452 (144%)	1,058 (338%)
Coldwater	319	94 (29%)	230 (72%)	389 (122%)	166 (52%)	607 (190%)
Spilus	641	149 (23%)	230 (36%)	359 (56%)	188 (29%)	561 (88%)
Thompson	120	398 (332%)	230 (192%)	3,164 (2,637%)	173 (144%)	4,944 (4,120%)
Thompson total	214	297 (139%)	230 (107%)	1,150 (537%)	195 (91%)	1,796 (839%)

Correlations between our empirical smolt carrying capacity estimates and two key parameters used in the Riley et al. (1998) model to predict smolt yield, estimated mean smolt age and fry-to-smolt survival ($r = 0.62$ and -0.58 , respectively), were opposite to expectations: we observed the highest smolt yields per km in the smaller Thompson River tributaries whereas the Riley et al. (1998) model assumed that these streams would have older mean smolt ages, and therefore lower fry-smolt survivals. As well, estimates of useable stream area per km in the Riley et al. model (and also in the Keogh smolt yield per useable area model) showed little correlation ($r = 0.21$) with our estimates of empirical smolt yield. Empirical smolt yield per km for the Keogh River at carrying capacity (230 smolts/km, Ward 2000) was the simplest modeling approach and performed the best at predicting empirical estimates of smolt yield in the Thompson River basin (Table 12).

A good relationship between our empirical estimates of smolt yield within the Thompson system and depth/stream size and substrate variables suggests potential factors affecting juvenile steelhead production at the stream scale. The highest prediction success resulted from a combination of the proportion of fine substrates and mean thalweg depths, which were negatively related to smolt yield, with $\ln(\text{Mean Thalweg Depth} * \text{Proportion Fines})$ explaining 92% of the variation in Beverton-Holt carrying capacity among the 6 streams of Table 12⁸.

4.0 DISCUSSION

4.1 Effectiveness of snorkeling and single-pass electrofishing for estimating parr abundance

Mark-recapture experiments suggested that night snorkeling detection probability for steelhead parr was consistently high and relatively stable among sites (Hagen et al. 2010), with few obvious outliers. The relatively low site-to-site variation in snorkeling detection probability estimates among sampling sites in the lower Thompson River basin can probably be attributed to several factors. First was the generally good water clarity in the study area streams in October. Our data suggests a minimum horizontal underwater visibility of 2.5-3 m is necessary for snorkelers to effectively count juvenile *O. mykiss* parr at night. Our finding that underwater visibility was not an important predictor of steelhead parr detection probability at levels ranging from 2.5-10 m probably reflects the fact that small fish such as juvenile steelhead allow snorkelers to approach to relatively close ranges at night before they attempt to flee. Snorkeling counts were conducted by highly experienced individuals, and this likely also contributed to consistent detection probability estimates. Perhaps the most important factor was that we conducted snorkeling counts at night, when juvenile steelhead parr are typically found resting on or near the substrate in near-shore areas of moderate depth and slow current, as opposed to during the day when they are more likely to be concealing themselves in the substrate or occupying drift-feeding positions further offshore. At night, snorkelers were able to closely approach individual fish, and observe them for extended periods. In the smaller streams in our study area, steelhead parr were sometimes observed in mid-channel areas where low-velocity microhabitats occurred as a result of low discharge and channel morphology, but snorkelers could readily survey these areas. In the larger streams in our study, the higher current velocities that made it more difficult for snorkelers to survey mid-channel areas likely excluded most steelhead parr from these areas as well.

In addition to being effective in all stream reaches of the lower Thompson River basin, snorkeling counts could be performed relatively quickly, making it possible to sample a large number of sites efficiently, and to sample large habitat units in their entirety. This meant that

⁸ Maximum site depth was substituted for thalweg depth for the Thompson River.

potential bias and inflated inter-site variance in fish abundance, which can arise from sub-sampling heterogeneous habitats such as pools (Hankin and Reeves 1988), was likely reduced. The total area of habitat that could be sampled per night by a two-person snorkeling crew (900-3,000 m²) exceeded, by three- to ten-fold, what can typically be sampled per day by a two-person electrofishing crew performing three-pass removals (300 m²). It is also important to note that we were able to use snorkeling to effectively sample all useable parr habitats in the lower Thompson River basin, with the exception of shallow riffles in the smaller tributaries. In contrast, backpack electrofishing would only be effective in the smallest tributary reaches of the study area when sampling sites spanning the entire stream channel. Our interpretation of steelhead parr habitat use in the lower Thompson River basin would have been very different if sampling had been limited to electrofishing only.

Depletion experiments suggested that single-pass electrofishing detection probability was also consistently high and relatively stable among sites for both steelhead parr and fry. Our finding that single-pass catches were relatively good predictors of three-pass depletion estimates is consistent with research done elsewhere (Lobon-Cervia and Utrilla 1993; Crozier and Kennedy 1994; Jones and Stockwell 1995). The potential for negative bias in the three-pass depletion estimates exists (Riley et al. 2003), which would result in underestimates of steelhead abundance in tributary riffles strata (i.e., detection probability would be overestimated). We assumed that the degree of negative bias in the three-pass estimates would be relatively modest because tributary riffle sites appeared well suited to electrofishing for reasons that included relatively high water conductivity levels, simple habitat structure, relatively short length and shallow depth, our use of block nets to enclose the sites, and the fact that steelhead are not overly benthic in their orientation (compared to bull trout, for example).

4.2 Productivity and carrying capacity of Thompson River steelhead

4.2.1 Considerations for the conservation and management framework

In the abundance-based precautionary management framework of Johnston et al. (2000), which has been adopted as a template for British Columbia steelhead management, the ‘target reference point’ (S_{TRP}) is a level of spawner abundance that it a very high proportion of maximum recruitment to maximize recreational fishing opportunities and other societal benefits. The ‘conservation concern threshold’ (S_{CCT}), is a reference point signaling an unacceptably low abundance and forcing mandatory reductions in fishing mortality, and is defined as spawner abundance at maximum sustainable yield (i.e. = S_{msy}). The lower spawner abundance threshold below which fishing is not permitted and management efforts are directed at stock rebuilding is termed the ‘limit reference point’ (S_{LRP}), and defined as the spawner abundance that would be able to recover to (S_{CCT}) within one generation under average environmental conditions in the absence of fishing (Johnston et al. 2000; Johnston 2013). The (S_{LRP}) is also intended to be sufficiently conservative to buffer populations from a high risk of extirpation (Johnston et al. 2002).

For the Thompson aggregate stock, over the 2001-2012 period represented by our data, deterministic estimates of S_{TRP} , S_{CCT} , and S_{LRP} based on the Ricker curve are 1,481⁹, 621, and 276 spawners, respectively. For the Nicola aggregate, estimated values are 1,013, 403, and 182 spawners for these same respective reference points.

Because they are expressed in terms of returning adults, the above estimates are functions of both the brood spawner-to-age-1+ parr stock-recruitment data and average ocean survival over the 2001-2012 period. It is important to note that the 2001-2012 period corresponds with low smolt-to-adult survival conditions in the ocean environment.

For the Nicola and Thompson aggregate stocks, Ricker estimates of R/S_{max} (2.6 and 2.7, respectively; Table 11) were lower than Ricker estimates derived from the entire adult-adult time series for Thompson River steelhead since the 1980s ($R/S_{max} = 4.4$; FLNRO unpublished data). The reason for this is that the parr abundance time series covers a recent period of very low ocean survival, whereas the adult time series covers the period from 1984-present, during which a decline in ocean survival has occurred. It is highly likely that the Thompson River steelhead aggregate, along with the majority of southern BC stocks, underwent a large decline in marine survival similar to that observed in the Keogh River during the late 1980s (Ahrens 2004, Smith 2000), which was approximately 3-fold to 4-fold in magnitude (Ward 2000). This decline in ocean survival is reflected in recent adult-to-adult stock-recruitment data, as well. In the analysis of Johnston (2013), time-varying estimates of R/S_{max} for the period of 2000 brood year to present ranged from 1.2 to 2.5.

The strategy recommended by Johnston (2013, and references therein) is to utilize long-term average ocean survival conditions as the basis for calculating the management reference points. Relative to periods of low ocean survival, long-term average survival conditions will correspond with a higher value of S_{CCT} , meaning that the conservation concern threshold will be more risk-averse.

In our analysis, the spawner-to-age-1+ parr stock-recruitment function and parr-to-smolt survival are assumed to be time-invariant. Delineating the density-dependent, freshwater production relationship for Thompson River steelhead permits us to utilize this relationship in exploring the effects of alternative smolt-to-adult ocean survival conditions on S_{LRP} and S_{CCT} . Note that S_{LRP} and S_{CCT} do not simply increase in proportion to increasing survival, and that after a certain point S_{LRP} declines as survival increases (Figure 8). Determining an appropriate value for long-term average age-1+-to-adult survival presents a challenge, as escapement estimates for the Thompson system are only available since 1984. Nonetheless, if brood year spawner estimates (FLNRO data on file) since that time are expressed as subsequent age-1+ parr recruits using the Ricker stock-recruitment relationship of section

⁹ S_{TRP} is assumed to be equivalent to Ricker R_{max} .

3.7¹⁰, then long-term average age-1+-to-adult (pre-fishery recruits) survival can be estimated as 1.05% for the Thompson aggregate as a whole, versus 0.62% for the 2001-2012 period (Table 11). For the Thompson aggregate stock, deterministic estimates of S_{TRP} , S_{CCT} , and S_{LRP} based on the Ricker curve and average parr-to-adult survival of 1.05% since the 1980s are 2,520, 879, and 221 spawners, respectively. For the Nicola aggregate, comparable estimates at 1.05% parr-to-adult survival were 1,819, 608, and 148 spawners, respectively. Even these estimates are likely to be biased low, because ocean survival estimates related to high adult returns in the mid-1980s cannot be generated (brood spawner abundance estimates are unavailable for the early 1980s).

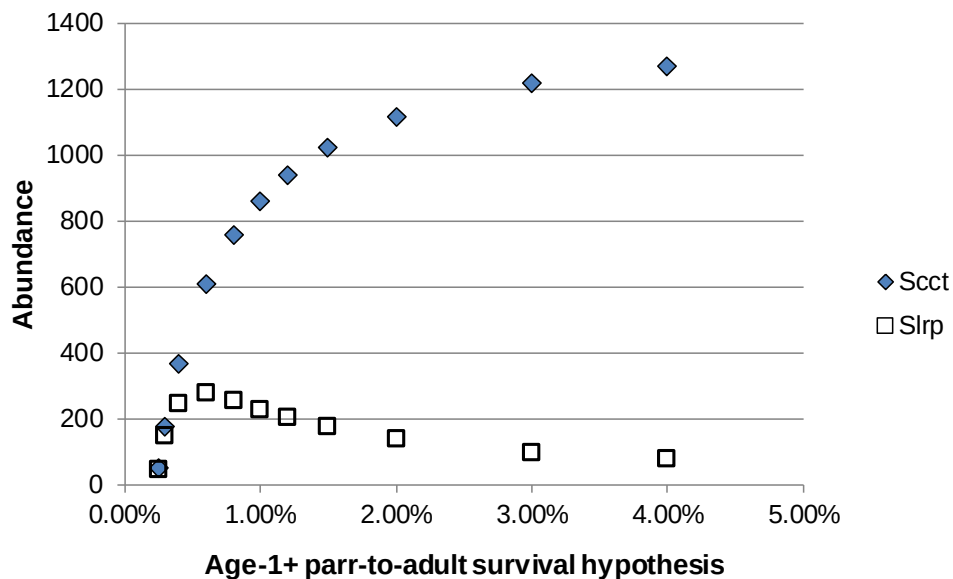


Figure 8. Estimates of management reference points ‘Limit Reference Point’ S_{LRP} and ‘Conservation Concern Threshold’ S_{CCT} , based on the Ricker adult-to-age-1+ parr stock recruitment relationship for the Thompson aggregate stock (see section 3.7), over a plausible range of potential age-1+ parr-to-adult survival rates.

It is important to note that under longer-term average parr-to-adult survival conditions the estimate of S_{LRP} for the Thompson aggregate is lower than that for the 2001-2012 period of low parr-to-adult survival (221 vs. 276 spawners, respectively), because productivity of the population has become lower. Given that recent low ocean survival conditions may persist, we recommend the more risk-averse strategy of employing a more conservative estimate of S_{LRP} .

¹⁰ Age-1+ recruits since 2001 are estimated from empirical sampling data in Table 6.

As indicated in the preceding paragraphs, uncertainty remains about what monitoring time frame best represents long term average survival, and how therefore how best to set appropriate levels of S_{CCT} , and S_{LRP} based on our stock-recruitment data (Figure 8). This is a difficult issue to resolve given persistent change in productivity exhibited by steelhead. In the interim, we feel that the parr data collected during our study support setting the S_{CCT} and S_{LRP} at 1,000 fish and 300 fish, respectively, for the Thompson aggregate stock. In the analysis of Johnston (2013), which does not incorporate the time series of steelhead parr data, S_{CCT} and S_{LRP} were computed to be 939 and 329, respectively, which are in relatively good agreement.

In addition, Johnston (2013) recommended a more conservative estimate of S_{LRP} to account for uncertainties in the data and in the viability of very small individual populations, proposing the use of the upper 80th percentile of the estimated distributions of S_{LRP} (431 spawners), which provides better protection for the stock. We recommend that the S_{LRP} be considered an ‘extreme’ conservation threshold for the stock that, if reached, should be associated with the immediate removal of all unnatural mortality and initiation of focused management actions directed at stock rebuilding. For the S_{LRP} to function as designed, and permit recovery of the spawning stock to S_{CCT} within one generation, effective conservation actions must be initiated with as little delay as possible. Agreement among management agencies and stakeholders, with respect to which actions will be triggered by spawner stock sizes that drop below the S_{LRP} , must therefore be in place before such low abundances are observed.

empirical estimates based on recent adult to parr stock recruitment patterns may not reflect the rearing potential of reaches T1 and T2? At low marine survival, density related dispersal processes may be insufficient to successfully disperse fry and parr into the linear ribbons and patches of cobble bars up and down reaches T1 and T2.

4.2.3 Errors in variables and time series bias

A number of conditions must be met for stock-recruitment analysis to be effective. One risk is that random measurement error in estimates of spawning stock will spread out the cluster of recruitment data points along the x-axis, creating the false impression of informative contrast, and the appearance that recruitment does not vary with spawning stock (Hilborn and Walters 1992). A manager in this scenario could unwittingly conclude that the system is at carrying capacity at current stock sizes. We know that the year-to-year contrast in escapements to the Deadman and Bonaparte rivers are real because spawner counts are made using calibrated electronic resistivity counters that provide relatively accurate and precise counts. However, for the Nicola stock, estimates of sampling error are more substantial relative to escapement estimates (median CV = 40% from 1999 to the present). Since the Nicola stock typically accounts for about 50% of entire Thompson aggregate estimate, sampling error is also substantial for the latter. In most years, the upper and lower

95% confidence intervals range within 70% and 30% of the annual aggregate escapement estimate, respectively. However, levels of escapement contrast for the Nicola and Thompson aggregate stocks (5.7- and 4.6-fold, respectively) were lower or comparable to those of the Deadman (7.2-fold) and Bonaparte (5.3-fold) stocks, suggesting that artificial magnification of the contrast in escapement estimates for the Nicola and Thompson aggregate stocks has not been substantial.

The Chinook Technical Committee of the Pacific Salmon Commission has published guidelines for stock-recruitment analyses (CTC 1999), wherein it is recommended that contrast in escapement be at least four-fold for the purpose of stock-recruitment analysis. Currently, contrast in escapement exceeds the minimum four-fold level recommended by the CTC for all stock groupings (Table 11), although the Thompson aggregate is still marginal relative to this standard. Hilborn and Walters (1992) suggested that measurement error and time series bias both are likely to be of low concern if contrast in escapement is at least 10-fold. This standard is not met by any of our Thompson stock-recruitment data, and therefore the study plan for future years identifies continued juvenile abundance monitoring in years of particularly high or low spawner escapement as a high priority.

Autocorrelation of stock-recruitment residuals over time (one form of time series bias) is probably not a great concern within our data set. Steelhead stock assessment in the Thompson River is now managed such that our annual parr survey is only scheduled in years when brood escapements provide desired levels of contrast. This approach should break up correlations among years.

4.2.4 Presence of rainbow trout and implications for future study

Similar to interior steelhead systems of the U.S. Pacific Northwest (Busby et al. 1996), Thompson River steelhead are sympatric with rainbow trout (non-migratory *O. mykiss*). Since steelhead are not distinguishable from the resident life-history form at the juvenile life stage, our estimates of steelhead parr abundance also include non-anadromous juveniles present in the reaches that we surveyed. The contribution of resident rainbow trout production to the total abundance of age-1+ juvenile *O. mykiss*, which could affect or obscure the stock-recruitment relationship, is a potential limitation of using adult-juvenile stock-recruitment data. For the Deadman and Bonaparte steelhead stocks, the steeply ascending portion of the stock-recruitment curve has not been revealed despite low spawning stock sizes (<100 spawners) and 7.2-fold and 5.3-fold levels of steelhead escapement contrast, respectively (Figure 7; Table 11). While this situation may indicate that current steelhead escapement levels are seeding the available rearing capacity of these systems, it may instead reflect resident rainbow trout production. Low parr utilization of Thompson reaches T1 and T2, downstream of the Deadman and Bonaparte systems, respectively, may be contrasting evidence suggesting that the rearing capacity available to these stocks is under-seeded. These observations raise the question of whether the contribution of resident rainbow trout to annual

parr standing stocks have been a significant factor obscuring the stock-recruitment relationships.

To address the potential confounding effect of resident contributions to our estimates of total parr abundance, in 2006 we initiated a study of the maternal origin (resident or anadromous mothers) of juvenile age-1+ *O. mykiss* within our study area using otolith microchemistry analysis (Hagen et al. 2012). Steelhead maternal origin strongly dominated parr samples from the Nicola system (93%-97%) and Thompson River mainstem (73%-86%), suggesting that the stock-recruitment relationship for the anadromous component is less likely to be obscured (Hagen et al. 2012).¹¹

In sharp contrast to the Nicola system and Thompson River mainstem, parr of resident maternal origin comprised approximately half the samples from the Deadman (47%-50%) and Bonaparte (47%) systems. In addition, trends in adult rainbow trout escapement to the Deadman River have been increasing since 1999 while steelhead escapements decline, suggesting that the contribution of resident mothers to the total parr standing stock is growing, and that parr of anadromous maternal origin may not face reduced intraspecific competition at low stock sizes (Hagen et al. 2012). Taken together, the combination of high abundance of resident-origin parr in the Deadman and Bonaparte Rivers, increased resident trout abundance in the Deadman River, and high parr abundance at low anadromous stock sizes for both systems suggests that the anadromous adult-parr stock-recruitment relationships are either being confounded (density-dependent population dynamics altered) or obscured by resident *O. mykiss* production.

Hagen et al. (2012) identified that addressing this issue in future years poses a considerable challenge. The most appropriate definition of spawning stock may be the sum of eggs from both steelhead and residents. Under this scenario, estimates of resident female spawner abundance and body size (requiring sampling of returning resident spawners in addition to detailed validation of resistivity counters) are required to derive estimates of resident egg deposition. However, even if these estimates are incorporated into annual monitoring in the Deadman and/or Bonaparte Rivers, the rate by which parr from these systems become smolts remains unknown, meaning estimates of anadromous recruitment also would remain unknown without otolith microchemistry analysis of either smolt or adult steelhead samples (Hagen et al. 2012). To address this issue, otolith sampling from post-

¹¹ Annual densities of age-1+ *O. mykiss* parr in the Thompson River mainstem downstream of the Nicola River confluence (Figure 1; reach T3) average 28-fold and 6-fold greater than those in the two mainstem reaches of the Thompson River above the Nicola (reaches T1, T2, respectively). Although the association of steelhead parr in the Thompson River downstream of the Nicola River with the Nicola River spawning population has not been confirmed (analysis pending; Hagen et al. 2012), the pattern of increased parr abundance below the Nicola, in addition to the dominance of the Thompson River sample by parr of anadromous maternal origin, support the inclusion of these fish in the Nicola aggregate for steelhead stock-recruitment analysis.

spawning, adult steelhead within the watershed has been recommended for future. Collecting otolith samples from post-spawning steelhead poses a considerable challenge, however, and efficient methods have yet to be worked out.

4.3 Associations of juvenile steelhead abundance with habitat, spawning distribution, and human activity.

We observed high spatial diversity in steelhead parr densities among streams and reaches within the study area, but the observed pattern was relatively consistent from year-to-year. Among tributary reaches, the highest parr densities occurred in secondary tributaries (Spius Creek and Criss Creek) which were steeper, had larger bed material relative to the size of their channels, had smaller channel widths relative to wetted widths (i.e., channels were more stable and confined) and were less impacted by floodplain agriculture and cattle grazing. Lowest parr densities occurred in lower gradient reaches in larger tributaries (upper Nicola, upper and lower Bonaparte) characterized by small bed material, with a much higher proportion of fines, and low structural complexity. However, the Deadman River supported moderate parr densities, despite, to some extent, possessing these same habitat characteristics.

In contrast to that in the tributaries, the pattern in parr abundance among reaches in the Thompson River mainstem did not appear to be strongly associated with habitat. Although, the lower canyon reach (T3; Figure 1) is steeper in gradient and contains coarser bed material on average, the upper (T1) and middle (T2) reaches of the Thompson River nonetheless contain extensive amounts of similar habitat (i.e., large unembedded substrate, optimal depth and current velocity), and have the same water temperature, hydraulic regimes, and fish assemblages as the lower canyon reach. Despite this, mean parr densities in the lower canyon reach (located downstream of the Nicola River mouth) were 6-fold and 11-fold higher than those in the upper (T1) and middle (T2) reaches. In some years, steelhead parr were nearly absent from the upper reach (Figure 5a). Given that steelhead do not appear to spawn directly in the Thompson River mainstem (McGregor 1986), we suspect that the distribution of parr in the mainstem is largely a result of dispersal patterns from natal tributaries. At the outset of the study, we were not surprised to find high parr densities downstream of the Nicola confluence. We do not have an explanation for the low utilization of the Thompson River mainstem upstream of the Nicola, other than the possibility that under current low marine survival and low spawner numbers, density-related dispersal processes are insufficiently strong to seed the available rearing habitat of these reaches as discussed in Section 4.2.4.

Our analysis of habitat effects on parr abundance at the site level suggested the same factors that appeared to be important influences at the reach level. Parr abundance was positively correlated with substrate size and mean depth, and negatively correlated with distance from the stream mouth. As well, within the tributaries, parr abundance was higher in deep habitats (runs and pools) relative to shallow ones (riffles). Habitat features that describe trout and salmon distribution and abundance have been a common area of research. While

the habitat factors predicting steelhead parr abundance in the lower Thompson River are consistent with findings for interior steelhead populations elsewhere, there are unique aspects to the distribution we observed that deserve comment.

Our finding that sites closer to the mouth of each stream had higher abundances may be more than simply a matter of greater wetted widths providing more useable area per unit length. Studies of resident trout in streams have identified optimal zones of channel gradient, stream size, and elevation where trout production is best (Elser 1968; Lanka et al. 1987; Kruse et al. 1997). In our study, however, large variation in these variables among habitats ranging from the Thompson River mainstem to Spius and Criss creeks did not explain our finding of high parr densities in each. It is possible that the anadromous nature of the steelhead populations influences their distribution to downstream versus upstream locations irrespective of these factors. In streams in Idaho, substantial numbers of juvenile steelhead and Chinook salmon move downstream in the fall, with movements peaking in September (Chapman 1966; Bjornn 1971). Moreover, as juvenile salmonids become larger they select faster and deeper water (Everest and Chapman 1972), which, in the case of deep water at least, is likely to be more prevalent in downstream locations. Higher parr densities in the downstream reaches may also reflect movement of age-0+ fish from upstream spawning sites during the previous fall.

Field and laboratory tests by Bjornn (1971) suggested that the capacity of Idaho streams to provide cover in the form of interstitial spaces in the substrate was an important factor determining whether juvenile steelhead remained in a stream section as winter approached. Juvenile steelhead entered substrate interstices as water temperatures declined towards winter, and if larger, unembedded substrate was not present they left in order to find it (Bjornn 1971). Substrate is larger in downstream reaches of Thompson and Nicola rivers relative to upstream reaches. Chapman (1966) suggests other ecological requirements of juvenile steelhead that contribute to their association with larger substrates. Territories defended by juvenile steelhead are smaller when visual isolation from other conspecifics is provided, a situation more likely to occur in larger substrate. The prevalence of larger substrates in areas of swifter flow, and therefore a higher density of drift-borne insects, may also be a factor, as may be the escape cover that unembedded, larger substrates provide from predation.

Anthropomorphic channel alterations can have a substantial effect on stream habitat quality, generally reducing habitat complexity and trout abundance (e.g. Elser 1968). Extensive agriculture, cattle grazing and transportation corridors adjacent to and within the floodplains of the Coldwater, Deadman, Bonaparte rivers, and the upper reach of the Nicola River have resulted in a reduction in riparian vegetation, and consequently reduced resistance to channel widening, reduction in stream velocity and substrate particle size, channel dewatering, and elevated summer temperatures. Climate change and water diversions for

irrigation are also likely to have contributed to reduced streamflows, higher summer temperatures, and reductions in available habitat in some reaches. The carrying capacity of these stream reaches for steelhead production may have been significantly reduced relative to historic levels. Spius Creek and Criss creeks, and the lower reaches of the Nicola and Thompson rivers are protected from habitat degradation to a greater degree by virtue of their channels being more confined, and in the case of Spius and Criss Creeks, by their location in less developed, forested valleys in the upper portions of the basin.

The distribution of spawning can also have a major influence on juvenile distribution (Beard and Carline 1991). It is likely that the dramatic increase in juvenile *O. mykiss* density in the Thompson River downstream of the Nicola River confluence, for example, is a result of recruitment from the Nicola system (see section 4.4). In other areas of the lower Thompson River basin (Bonaparte River, and the upper portions of Coldwater River, Spius and Criss creeks) it is possible that spawning is too limited to fully seed suitable parr habitat. This could be caused by poor suitability for spawning, or limitations caused by the necessity of lengthy migrations during periods of high discharge and low water temperatures in spring¹².

For some fish populations, density-independent mortality factors are more important than density-dependent processes in regulating abundance in less physically stable or suitable environments. In highly suitable rearing habitats at the core of the species' range, density-dependent or compensatory mortality is thought to be prevalent (Larkin 1956; Chapman 1966; Elliott 1987). We found that year-to-year variability in steelhead parr abundance was indeed greater in low quality 'marginal' sites, characterized by shallow depths and fine bed materials, as compared to high quality 'core' rearing sites. This suggests that the practice of locating sites only in habitats judged to be 'optimal' or 'representative' – a strategy commonly used by fisheries biologists to address spatial heterogeneity in fish abundance – may result, not only in biased population estimates, but also in underestimates of variance among sites and among years, with the result that meaningful changes in total abundance over time may go undetected. We suggest the use of a random or systematic sampling design instead, as is generally recommended for research in population ecology (Krebs 1999).

We found no evidence that variation in steelhead parr and fry abundance among years was negatively impacted by Chinook salmon fry abundance. In fact, a positive correlation between steelhead and Chinook fry abundance suggests that similar density-independent environmental factors affect both populations in the lower Thompson River. Research by Everest and Chapman (1972) suggests that only juvenile steelhead and Chinook of the same size used the same physical space in streams, and that very different emergence timing resulted in body size differences that limited the potential for interspecific competition.

¹² Adult steelhead returning to spawn in Thompson River tributaries, arrive in late fall, overwinter in the mainstem, complete their migration to tributary spawning locations the following spring (McGregor 1986).

Moreover, they found that in the presence of Chinook of the same size, steelhead did not change their habitat preference.

4.4 Utility of steelhead habitat capability modeling

Johnston et al. (2000) suggested that conducting juvenile steelhead stock assessment was not feasible over large spatial scales and many stocks, and that habitat-based production models were needed to provide estimates of carrying capacity. We found, however, that habitat capability models employed previously in British Columbia to estimate steelhead carrying capacity (smolt yield at carrying capacity, e.g., Tautz et al. 1992; Riley et al. 1998) were in some cases poor predictors of empirical estimates for streams in the lower Thompson River basin. In the majority of cases, the habitat capability models underestimated smolt yield in the smaller streams and overestimated yield in the larger ones (Table 12).

There are numerous factors that likely contributed to discrepancies between model predictions and empirical estimates of smolt yield in Thompson River tributaries. With respect to habitat capability models based on empirical data from the Keogh River, differences in seasonal hydrology, habitat characteristics, and resultant productivity between this small coastal stream and streams within the dryer lower Thompson River basin likely played a role. Other factors not accounted for by the habitat capability models, but likely important to predicting differences in productivity among streams in large interior watersheds include ecoprovince (e.g., Cascade Mountains versus southern interior plateau), adjacent land use, spawner distribution, valley geomorphology (e.g., alluvial floodplain versus confined canyon), climate, water temperature and its effect on fish species assemblage, and winter ice accumulation. In large interior river basins these factors can vary greatly among streams, and even within stream reaches.

In the case of the Thompson River mainstem, habitat capability models that relied on stream area or useable stream area as a basis for predicting carrying capacity (Table 12) greatly overestimated smolt yield. There are two potential reasons. First, models did not take into account juvenile dispersal dynamics, which, as discussed previously, likely contributed to a lack of juvenile production in the upper two reaches of the mainstem, despite the abundance of potentially useable habitat there. Second, they relied on empirical carrying capacity data from much smaller streams, where juvenile habitat differs greatly from that in large rivers such as the Thompson. In small streams useable parr habitat extends across a greater proportion of the channel cross-section, relative to the Thompson River where useable habitat is constrained to a potentially narrow band along each bank. Modeling smolt yield based on stream area or useable stream area appears to be problematic in systems that include larger mainstem reaches. Estimates of useable stream area per km for individual Thompson River streams in the Riley et al. (1998) model were not correlated with observed smolt yields for these streams, suggesting that key elements of habitat quality were not accurately represented.

If habitat capability models are to provide useful estimates of smolt yield at carrying capacity, for defining conservation reference points (e.g. Johnston et al. 2000) or for other management purposes, predictors of habitat capability need to be more reliable than those that have been identified to date. In this study, we have identified habitat factors that were significant predictors of steelhead abundance in the lower Thompson River basin (substrate size, mean thalweg depth, habitat type). A similar approach may have utility in other large river basins as well. The challenge in developing a predictive tool is to compile an extensive multi-stream database consisting of unbiased empirical estimates of parr or smolt yield at carrying capacity, together with estimates of habitat variables that are amenable to meta-analysis. Such data already exist for a limited number of small streams across BC with steelhead and rainbow trout populations (e.g. Ward and Slaney 1993). Comparable information from larger stream reaches is more limited but future studies, employing methods described for this study or alternatives, are likely to occur (e.g. Decker and Hagen 2009; Korman et al. 2010b).

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Appendix 1. Length-at-age data collected for age-0+ to age-3+ juvenile *O. mykiss* in the lower Thompson River mainstem and tributaries during 2001-2012 ($N = 663$). Values shown for each fork length (mm) category are frequencies.

Fork length	Bonaparte 0 1 2	Criss 0 1 2 3	Coldwater 0 1 2 3	Deadman 0 1 2 3	Nicola 0 1 2	Spius 0 1 2 3	Thompson 0 1 2 3
<45		1	1	2		1	
45-49		3		1	3		
50-54		2	1	3	1	2	
55-59		3			2	2	
60-64	2	1	1	1	2		
65-69	1				4		
70-74		1	1	3	7	1	
75-79		1 1	4	12 1	10	1	1
80-84		4 8	4	11 3	18	1	2
85-89	1	9	11	9 3	12 1	3	2 2
90-94	1	10	13	1	6 3	5	2 1
95-99		15	4	2	2 9	2	2
100-104	1	3	1	1	2 4	3	1
105-109	1	4	5 1		5	6	2
110-114	3	4	5		4	6	2
115-119	3	3	15	1	5	8	2
120-124	3	4	8 1	1	5	14	5 2
125-129	1	2	10 2	2	4 1	11	8
130-134	3	2 2	4 3	3	2	11	1
135-139		1 2	1 2	2	6 2	4 1	3 1
140-144	1	1 7	2 2	1 1	3	4 4	2
145-149	1	1 3	1	1	3	2 2	3
150-154		3	4	1	1 1	1 6	5 3
155-159	2	1 4 1			2 1	5	1 3
160-164	1	3	2		1	1 3 1	4 2
165-169		1	4			4	2
170-174		1		1	1 1	1 1	2
175-179	1						1 1
180-184							3
185-189							4
190-194							1
195-199		3	1			1	1
200-204							
205-209		1	1				3
210-214						1	2
215-219							
220-224							1
225-230				1			
>230							2

Appendix 2. Definition of variables of the hierarchical Bayesian model used to estimate juvenile steelhead abundance in the lower Thompson River system.

Variable	Description
Data	
$r_{i,g}$	Marks detected at snorkeling mark-recapture site i, channel width-fish size strata g
$m_{i,g}$	Marks released at mark-recapture site i, strata g
$d_{i,p,g}$	Catch at 3-pass removal site i on pass p for strata g
$c_{j,g}$	Fish detected at index site j for strata g
l_j	Stream length for index site j
h_s	Total stream length in stream-reach-habitat strata s
Site-Specific Parameters	
$\theta_{i,g}$	Estimated detection probability at mark-recapture or 3-pass removal site i for strata g
$\theta_{j,g}$	Simulated detection probability for index site j for strata g
λ_j	Estimated density (fish/m) at index site j
Hyper-Parameters	
$\mu_{\theta,g}$	Mean of beta hyper-distribution for detection probability for strata g
$\tau_{\theta,g}$	Precision of beta hyper-distribution for detection probability for strata g
$\mu_{\lambda,s}$	Mean of normal hyper-distribution for log fish density for strata s
$\tau_{\lambda,q}$	Precision of normal hyper-distribution for log fish density for lumped strata q
Derived Variables	
$\alpha_{i,g}$	Parameter for beta hyper distribution of detection probability for strata g
$\beta_{i,g}$	Parameter for beta hyper distribution of detection probability for strata g
$N_{i,g}$	Initial abundance at 3-pass removal site i for strata g
$n_{i,p,g}$	Number of fish in 3-pass removal site i for strata g prior to pass p
$N_{j,g}$	Abundance at index site j sampled by strata g
NS_s	Total abundance across all index sites in strata s
Nu_s	Total abundance in unsampled stream length line in strata s
Nt_s	Total abundance in habitat strata s
Nt_t	Total abundance across all strata in stream t
Nt	Total abundance across all streams
Indices and Constants	
i	Index for snorkeling mark-recapture site
p	Index for electrofishing removal pass number
j	Index for snorkeling and electrofishing index sites
g	Index for gear type-channel width-fish size strata
s	Index for stream-reach-habitat strata
q	Index for lumped groups of s across streams and reaches within habitats
t	Index for stream

Appendix 3. Equations of the hierarchical Bayesian model used to estimate juvenile steelhead abundance in the lower Thompson River system. See Appendix 2 for definitions of model parameters, constants, and subscripts. Lower case Arabic letters denote data or indices (if subscripts). Capital Arabic letters denoted derived variables, which are computed as a function of estimated parameters. Greek letters denote estimated parameters. Parameters with Greek letter subscripts are hyper-parameters.

Detection Model

$$(1) \quad r_{i,g} \sim \text{dbin}(\theta_{i,g}, m_{i,g})$$

$$(2) \quad d_{i,p,g} \sim \text{dbeta}(\theta_{i,g}, n_{i,p-1,g})$$

$$(3) \quad n_{i,p,g} = N_{i,g} (1 - \theta_{i,g})^{p-1} \theta_{i,g}$$

$$(4) \quad \theta_{i,g} \sim \text{dbeta}(\alpha_g, \beta_g)$$

Population Model

$$(5) \quad \theta_{j,g} \sim \text{dbeta}(\alpha_g, \beta_g)$$

$$(6) \quad c_{j,g} \sim \text{dbin}(\theta_{j,g}, N_{j,g})$$

$$(7) \quad N_{j,g} \sim \text{dpois}(\lambda_j l_j)$$

$$(8) \quad \log(\lambda_j) \sim \text{dnorm}(\mu_{\lambda,s}, \tau_{\lambda,q})$$

$$(9) \quad Ns_s = \sum_g \sum_{j \in r} n_{j,g}$$

$$(10) \quad Nus_s = \exp[\mu_{\lambda,s} + 0.5\tau_{\lambda,q}^{-1}](h_r - \sum_{j \in s} l_j)$$

$$(11) \quad Nt_s = Ns_s + Nus_s$$

$$(12) \quad Nt_t = \sum_{s \in t} Nt_s$$

$$(13) \quad Nt = \sum_t Nt_t$$

Appendix 3, continued.

Priors and Transformation

$$(3.14) \quad \begin{aligned} \mu_{\theta,g} &\sim \text{dunif}(0,1) \\ \sigma_{\theta,g} &\sim \text{dhcauchy}(0,0.5) \end{aligned}$$

$$(3.15) \quad \begin{aligned} \tau_{\theta,g} &= \sigma_{\theta,g}^{-2} \\ \alpha_g &= \mu_{\theta,g} \tau_{\theta,g} \\ \beta_g &= (1 - \mu_{\theta,g}) \tau_{\theta,g} \end{aligned}$$

$$(3.16) \quad \begin{aligned} \mu_{\lambda,s} &\sim \text{dnorm}(0, 0.1.0E-6) \\ \sigma_{\lambda,q} &\sim \text{dhcauchy}(0,0.5) \end{aligned}$$

$$(3.17) \quad \tau_{\lambda,q} = \sigma_{\lambda,q}^{-2}$$

Appendix 4. Summary of data deficiencies and alternate approaches taken with respect to estimation of parameters and hyper-distributions in the Hierarchical Bayesian Model (HBM) used to estimate juvenile steelhead standing stocks in the lower Thompson River system during 2001-2012.

1. *Snorkeling detection probability for large-sized parr (>170 mm) in small channel streams and for small-sized parr (<100 mm) in large channel streams.* In each case, there relatively few of fish of each size class present at mark-recapture sites in the respective stream categories, resulting in too few fish being marked and subsequently detected by snorkelers. This led to an insufficient amount of data to for the HBM to reliably estimate variance in detection probability. These deficiencies were addressed by substituting estimates of variance in detection probability for large parr in large channel streams and small parr in small channel streams (sample sizes were much larger for these strata and parameters could be reliably estimated).

2. *Estimation of variance in fish density for individual strata when the number of index sampling sites is relatively low (< 10) for many strata.* Estimates of variance in fish density produced by the HBM were unstable for a number of individual strata due to low number of sites sampled. This was addressed by pooling abundance data among similar strata for the purpose of estimating within-strata variance in fish density only (mean fish density was still estimated independently for each strata). For small-sized parr, variance in fish density was estimated with strata lumped into just two groups: tributary riffle strata, and tributary run strata + Thompson mainstem strata. For medium-sized (100 to 170 mm) and large-sized parr, strata were lumped into three groups: tributary riffle strata, tributary run strata, and Thompson mainstem strata.