

UNIVERSITY OF CALGARY

Migration, Diel Movement and Habitat Use of Juvenile

Bull Trout (*Salvelinus confluentus*)

By

Craig J. Mushens

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

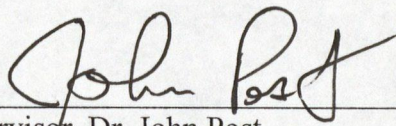
CALGARY, ALBERTA

APRIL, 2003

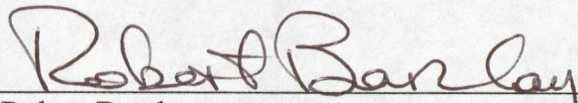
© Craig J. Mushens 2003

UNIVERSITY OF CALGARY  
FACULTY OF GRADUATE STUDIES

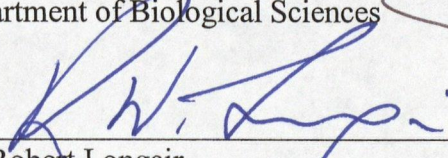
The undersigned certify that they have read and recommend to the Faculty of Graduate studies for acceptance, a thesis entitled "Migration, Diel Movement and Habitat Use of Juvenile Bull Trout (*Salvelinus confluentus*)" submitted by Craig J. Mushens in partial fulfillment of the requirements for the degree of Master of Science.



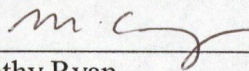
Supervisor, Dr. John Post  
Department of Biological Sciences



Dr. Robert Barclay  
Department of Biological Sciences



Dr. Robert Longair  
Department of Biological Sciences



Dr. Cathy Ryan  
Department of Geology and Geophysics

April 28/03  
Date



## **Abstract**

I investigated the movement and behaviour of individual juvenile bull trout over a range of temporal and spatial scales in Smith-Dorrien Creek. A strong correlation exists between the upstream migration of adult bull trout and the downstream migration of juveniles. The upstream migration of adult bull trout is regulated by stream flow and positive changes in temperature, while the downstream migration of juveniles is positively related to growth rate. Juveniles in the stream display either mobile or sedentary behaviour patterns. Sedentary juveniles display minimal displacement within the stream (median 12.1 m); showing fidelity to a particular “home stone” for daytime refuge, while maintaining a home range extending up to 200m. Diel differences in habitat use and movement exist between night and day. Presence of adult bull trout in the stream during spawning can negatively affect habitat use and behaviour of juveniles, possibly leading to limited habitat availability and reduced growth rates.

## Acknowledgements

Many people and organizations played key roles in helping me complete this thesis. This project was funded by a cooperative partnership between the Alberta Conservation Association and TransAlta Utilities. I would like to thank the staff and administration of Kananaskis Country and Peter Lougheed Provincial Park, for providing me and my field assistants with a warm dry place to hang our hats and the opportunity to be part of a community. Dave Hanna, I think I still owe you for a few lost bets. My field crew over the years was trustworthy and didn't complain too much about the many long nights (and days) of work; thank you Garland Jonker, Suzanne Earle, Jean-Yves Dionne, Duane Fizer and Mike Logan. There were also many volunteers, eager to sacrifice some valuable sleep to see what fish do at night, or net that "big one". Judy Mappin and Grace LaBelle were my friendly and helpful contacts at Barrier Lake Field Station. I thank my supervisor, John Post, for being a patient man and providing alternate views or approaches which helped to broaden the way I perceive the finer details.

B.K. Thompson and Andy Paul were a welcome source of procrastination over the years but were also my nagging conscience and an overwhelming source of knowledge. My parents have always supported my work and I appreciate the opportunities I had by being allowed to choose my own direction. My siblings, Scott, Garry and Heather, have always harassed me, possibly because their jobs don't allow them to stand in a creek and fish, but were always there to help out. And finally I especially thank my loving wife, Kathleen, who still married me even though my thesis

wasn't completed by the wedding. She has been a grounding influence, keeping me focused on the goal and supporting me all the way.

## Table of Contents

Abstract.....	iii
Acknowledgements.....	iv
Table of Contents.....	vi
List of Tables .....	viii
List of Figures .....	x
1 Chapter 1 – Introduction .....	1
1.1 Migration / Movement.....	1
1.2 Study Species Background .....	2
1.3 Thesis Organization .....	4
2 Chapter 2 – Effects of environmental variables and inter-cohort interactions on adult and juvenile bull trout migration.....	8
2.1 Introduction.....	8
2.2 Methods .....	11
2.2.1 Study Site.....	11
2.2.2 Migration.....	12
2.2.3 Temperature .....	13
2.2.4 Discharge .....	14
2.2.5 Moon Intensity .....	14
2.2.6 Growth Rates .....	15
2.2.7 Inter-Cohort interactions.....	18
2.3 Results.....	18
2.3.1 Adult Upstream Migration.....	18
2.3.2 Juvenile Downstream Migration.....	21
2.4 Discussion.....	23
2.4.1 Adults.....	23
2.4.2 Juveniles.....	26
3 Chapter 3 – Diel and seasonal movements of juvenile bull trout and refuge preferences .....	47
3.1 Introduction.....	47
3.2 Methods .....	51
3.2.1 Study Area .....	51
3.2.2 Long-term habitat use and movement.....	51
3.2.3 Short-term habitat use and movement .....	53
3.2.4 Analysis.....	56
3.3 Results.....	56
3.3.1 Home range / Restricted Movement .....	56
3.3.2 Distance Moved Between Day and Night.....	59
3.3.3 Predator Avoidance.....	62
3.3.4 Habitat Preference.....	63

3.4	Discussion.....	63
4	Chapter 4 – Effect of adult presence on juvenile behaviour and habitat use .....	86
4.1	Introduction.....	86
4.2	Methods .....	89
4.2.1	Study Area .....	89
4.2.2	Field Technique .....	89
4.2.3	Analysis.....	91
4.3	Results.....	93
4.3.1	Habitat Depth Use.....	93
4.3.2	Index of Vigilance.....	95
4.4	Discussion.....	96
	Chapter 5 - Summary .....	108
	Bibliography .....	111

## List of Tables

Table 2.1	Logistic regression models relating the chance of a juvenile migrating downstream as a function of its mean standardized growth rate deviation (Growth) or a constant. Twice the difference in negative log-likelihoods between the full model (constant + Growth) and either of the two simpler models, with one parameter removed, follow a chi-square distribution with one degree of freedom. A significant chi-square value (i.e. $P < 0.05$ ) indicates the removed parameter significantly contributed to the model.....	31
Table 2.2	Analysis of variance (ANOVA) of size between migrant and instream bull trout for each age class (age-2 and age-3), and both years (1998 and 1999).....	32
Table 3.1	Summary of telemetry tag deployment and fish characteristics. Actual number of tags used in analysis (in parentheses) was lower as two tags died within five days of deployment and two tags showed no movement throughout the life of the tag and is suspected that these fish died or the tags were shed. ....	72
Table 3.2	Numbers of bull trout in each sample cohort (bold) and number known to be alive/present in study section after initial capture. Each sample cohort represents untagged fish captured within a particular sample event. Recapture values from a total of nine sampling events after first capture were used to calculate capture efficiency.....	73
Table 3.3	Radio-tagged fish grouped with respect to movement (range < or > 50 m), overall displacement (< or > 50 m), and fidelity to daytime refuges (low > 4, high <= 4). The combination of low movement and high displacement is not possible as displacement cannot exceed movement. Fish with high movement, high displacement and high fidelity are generally fish that showed low movement and displacement within the stream and then migrated downstream to Lower Kananaskis Lake. ....	74
Table 3.4	Summary statistics of $\chi^2$ tests on various habitat variables between day and night. Critical P value is 0.05. ....	75
Table 4.1	Habitat measurements of sections 2 and 3 of Smith-Dorrien Creek, and James Walker Creek (JWC). Depth and habitat unit composition data not collected for JWC. ....	100
Table 4.2	Results of 3 way analysis of covariance (ANCOVA) determining whether juvenile bull trout used shallower habitat (log depth), while adults were present in the stream (Adult Presence), compared to both before and after adults were present. To remove any bias of larger juveniles using deeper habitat, fork length was introduced as a covariate. Refer to Figure 4.3 for a graphical representation of these results...	101



Table 4.3	Results of two way analysis of covariance (ANCOVA) determining whether vigilance of juvenile bull trout in sections 2 and 3 (include JWC), differed in response to the presence or absence of adult bull trout (see Figure 4.4) with moonlight intensity as a covariate.....	102
-----------	--	-----

## List of Figures

Figure 1.1	Map of Smith-Dorrien Creek and Lower Kananaskis Lake. ....	6
Figure 1.2	A generalized ontogenetic sequence (following numbers in circles) of an adfluvial bull trout population. (1) Larvae and fry undertake a trophic migration to their first feeding habitat. (2-3) Juveniles undertake daily migrations between feeding habitat and refuge habitat. (4) Juveniles/Sub-Adults undertake a migration out of the rearing stream into a lake system. (5-6) Adults/Sub-Adults in lake may undertake trophic migrations and return to survival habitat on a daily basis. (7) Adults undertake fall spawning migrations into spawning habitat in tributary streams and return to lake. Adapted from Northcote (1997).....	7
Figure 2.1	Map of Smith-Dorrien Creek indicating the location of the fish fence. ....	33
Figure 2.2	Schematic of fish fence and trap on Smith-Dorrien Creek.....	34
Figure 2.3	Plot of fork length of juvenile bull trout aged from otoliths against day of the year when sampled. The slope in the regression equation for each age class corresponds to the daily growth rate. The regression line and equation for age-3 fish is estimated from the average of the slopes of age-1 and age-2 fish.....	35
Figure 2.4	Timing of upstream migration of adult bull trout and downstream migration of juveniles in Smith-Dorrien Creek caught in the trap from 1 August until mid-October. In 1998, a 4 m opening in the fence was present from 31 July to 5 August (shaded area), during which at least 465 adults moved upstream. A similar breach in 1999 from 11 to 20 August is suspected to have allowed 90 adults to move upstream. ....	36
Figure 2.5	Cumulative percent of upstream migration of adult bull trout over time for each year. Points within each year represent cumulative migration levels of 5, 25, 50, 75 and 95% respectively. ....	37
Figure 2.6	Schematic of the cyclical relationship between discharge and temperature each year. This figure can be broken into four key events throughout the season: 1. increasing temperature with low flows in late winter / early spring, 2. rapid increase in discharge in late spring / early summer with the onset of spring runoff. Temperature remains relatively constant due to the mediating effects of the snow pack, 3. decline in discharge in late summer as the snow pack declines, and extended daylight leads to maximum daily temperatures, 4. steady decline in discharge and daily temperatures as photoperiod is reduced into the winter where temperature and flow remain low and constant. ....	38

- Figure 2.7 Seasonal discharge-temperature relationship in Smith-Dorrien Creek from 15 July to 30 Sept. each year (1996 (a) to 2000 (e)). Symbols represent the weighted mean migration temperature and discharge (Quinn et al. 1997) over the period when the associated proportion of adults moved into the creek, i.e. solid circle represents weighted mean temperature and discharge over the period that the first 5% of adults moved into the creek. Arrows indicate general direction of discharge-temperature relationship. Horizontal dashed lines indicate level where discharge equals  $3.5 \text{ m}^3 \cdot \text{s}^{-1}$ . ..... 39
- Figure 2.8 Number of adult bull trout migrating upstream each night in relation to maximum daily temperature. Linear regression best fit lines are displayed with corresponding R-squared values. In all years, a significant positive relationship was observed between temperature and the number of adults migrating upstream. .... 40
- Figure 2.9 Number of adult bull trout migrating upstream each night in relation to moon intensity and moonlight duration. At 100%, moon intensity is synonymous with a full moon and at 0% with a new moon. Moonlight duration is measured as the amount of time that the moon is in the sky between evening and morning twilight. Shaded areas in 1998 and 1999 indicate periods when the trap was inoperable. .... 41
- Figure 2.10 Weekly growth rates of juvenile bull trout and mean weekly temperatures in Smith-Dorrien Creek for 1998 and 1999. .... 42
- Figure 2.11 Proportion of juveniles migrating downstream in a) 1998 b) 1999 and c) both years combined, relative to the difference of the weekly growth rate from the mean. Due to unequal variance between months, growth rates were standardized by dividing by standard deviation. For individuals with multiple measurements, the standardized growth rate was averaged. Based on results from log likelihood analysis, the line predicts the probability of a fish within each growth rate category migrating downstream. .... 43
- Figure 2.12 Standardized residual growth rates from the mean in 1998 and 1999 over the range of fork lengths sampled in Smith-Dorrien Creek. In 1998, growth rates were size dependent with larger fish having higher growth rates. Growth rates were not size dependent in 1999. .... 44
- Figure 2.13 Length-frequencies of juvenile bull trout captured in Smith-Dorrien Creek (lines) and juveniles captured migrating downstream out of the creek (bars) in 1998 and 1999. .... 45
- Figure 2.14 Cross-correlation plots between weekly upstream counts of adults and weekly downstream counts of juveniles for years 1996 (a) to 2000 (e). For example, in 1996 (a), the downstream migration of juveniles was positively correlated with the upstream movement of adults two weeks previous. The correlation value at lag zero

	is the Pearson correlation. The curved lines indicate 95% confidence levels for the significance of each correlation.....	46
Figure 3.1	Map of Smith-Dorrien Creek indicating locations of study sections 2 and 3. ....	76
Figure 3.2	a) Recapture rates of 10 sampling "cohorts" from the first recapture after initial tagging to the final sampling (total of 10 sampling periods). Each sample period is the corresponding sequential recapture period of each of the 10 cohorts. For example, sample period 1 contains the first recapture session of all 10 cohorts which vary in time depending on when each cohort was established (see Table 3.1). Error bars are standard deviation (SD). b) Weekly loss rate (proportion of fish lost between sample periods) of PIT-tagged bull trout throughout the 1998 sampling season. The last set of data points show low loss rate from late October 1998 to May 1999. Data are divided into two groups: open circles are migration after first capture (only one data point per date) and solid circles are the mean migration rate of all sampling "cohorts" active within a time period with SD error bars. Migration rates are highest for fish within the first time period after tagging.....	77
Figure 3.3	Frequency histogram of juvenile PIT-tagged bull trout and their distance from the initial point of capture for all data from 1998 and 1999. Distance bins are in 10 m intervals with the number indicated representing the upper limit of the bin. This figure was truncated at 500 m which contains 96% of all fish. Maximum distance measured by fish not migrating into Lower Kananaskis Lake was 4800 m. Solid line indicates a negative power relationship ( $y = 89.78 x^{-1.28}$ , $R^2 = 0.82$ ). ..	78
Figure 3.4	Overall distance moved within a 40-day period of PIT-tagged juvenile bull trout in relation to fork length of tagged fish. Data are separated into four groups: pre-adult (May-August), adult (August-October), post-adult (October), and migration (movement out of Smith-Dorrien Creek). There was no significant difference in distance moved with respect to size or to time period (except for migration). Note y-axis is on a logarithmic scale and no fish smaller than 75 mm in length received a PIT tag. ....	79
Figure 3.5	Comparison of overall range of movement of juvenile bull trout to overall displacement for radio-tagged (time scale < 22 days) and PIT tagged fish (time scale > 25 days). Overall range encompasses the distance between the most upstream and downstream locations that an individual fish was captured. Overall displacement is the distance between the point of capture and the final location where the individual fish was captured. Note axes are on a logarithmic scale, light dashed line indicates 1:1 line and heavy dashed line indicates 50 m displacement. Points on the 1:1 line indicate fish whose displacement equaled their range of movement. Points below the 1:1 line indicate fish that moved in both directions, reducing the overall displacement in comparison to the range. ....	80

- Figure 3.6 Relationship between nighttime range and daytime range for radio-tagged juvenile bull trout prior to downstream migration. Non-solid points indicate fish that eventually migrated downstream. Dashed line indicates 1:1 line. Note axes are on a logarithmic scale. .... 81
- Figure 3.7 Relationship between number of nighttime and daytime locations identified for individual radio-tagged bull trout. Nighttime locations were either equal to or more numerous than daytime locations. Larger points represent two values at that point. Dashed line indicates 1:1 line. .... 82
- Figure 3.8 Selection of graphs outlining various diel movement behaviours of radio-tagged bull trout. Each graph is referenced by the telemetry tag number and is accompanied with an indication of the number of day (D) and night (N) locations and overall displacement (Displ.). Note x-axis scales vary and each graph encompasses the entire life of a radio-tag. Numbers in brackets indicate displacement before downstream migration. .... 83
- Figure 3.9 Distance radio-tagged fish 149.260 moved when checked at five time intervals throughout the night on 6 October, 1999. The first sample time (20:30) is before dusk when no movement is expected. The second time is just after dusk (\*). The fish was normally checked between the second and third time period (around 23:00). Subsequent times cover the rest of the night and show that the fish moved throughout the night and that an assessment of no movement at one time does not mean that the fish does not move out to feed at a later time. The fish returned to the same daytime refuge at dawn. .... 84
- Figure 3.10 Comparison of habitat variables measured between day and night for 35 radio-tagged bull trout. Variables include cover types, stream velocity, substrate composition and stream habitat units. .... 85
- Figure 4.1 Map of Smith-Dorrien Creek indicating the location of the study sections 2 and 3, and James Walker Creek. .... 103
- Figure 4.2 Mean depth use of juvenile bull trout in Smith-Dorrien Creek for each sampling date in 1998 (a - c), and 1999 (d - f), in all three study sections: Section 2 (a and d), Section 3 (b and e) and JWC (c and f). Area between the dashed vertical lines indicates the time period when adults were present in Smith-Dorrien Creek. .... 104
- Figure 4.3 ANCOVA results comparing juvenile habitat depth (Log Depth) use in Smith-Dorrien Creek to the presence or absence of adults within the stream in Section 2 (a and d), Section 3 (b and e) and JWC (c and f) for both 1998 (a to c) and 1999 (d to f). To eliminate any effects that size may have on depth use, fork length was included as a covariate. In sections 2 and 3 in both years and JWC in 1998, log depth use was significantly lower when adults were present in the creek compared to

both pre- and post-adults. Log depth use was not different between time periods in JWC in 1999. Error bars are standard error (SE) .....	105
Figure 4.4 Daily discharge measurements ( $\text{m}^3 \cdot \text{s}^{-1}$ ) at the mouth of Smith-Dorrien Creek in 1998 and 1999. ....	106
Figure 4.5 Index of vigilance of juvenile bull trout in Smith-Dorrien Creek in both Section 2 and 3 in 1999. The index of vigilance is an effort to quantitatively assess the level of awareness that a juvenile bull trout has of its surroundings (within 0.2 m). The index is calculated as one minus the capture efficiency (proportion of fish successfully caught on first attempt). The time period between the vertical dashed lines indicates when adults had entered the creek.....	107



## **Chapter 1 – Introduction**

### **1.1 Migration / Movement**

Migration is a common phenomenon among plants and animals for which the magnitude can vary substantially both temporally and spatially. In animals, the time-scale involved may be hours, months or years (Begon et al. 1990), and the distance may vary from metres to hundreds or thousands of kilometres. Migration can occur on a daily basis or as an ontogenetic shift to take advantage of superior food resources, increased habitat availability, reduced predation risk or reproduction (Erkert 1982; Begon et al. 1990; Northcote 1997). Many species move from one habitat to another and back again repeatedly during their life. In general, migrations can be grouped according to temporal scale as diel, seasonal and annual/multi-annual cycles.

For most organisms, the environment is subject to rhythmic alteration. The rotation of the earth produces a 24-hour periodicity in light intensity, temperature and humidity. The revolution of the moon around the earth can also influence these rhythms by influencing nighttime brightness and the tides. Because the rhythms of animals mesh in different ways with the overall periodicity of the environment, the biotic factors of concern to each individual – food supply, competition for food, predator pressure – also vary on a daily, annual and in some cases, lunar basis. Therefore, a successful strategy for survival must include optimal adjustment of an animal's activity rhythm to these environmental periodicities (Erkert 1982). Individuals may move to maintain a constant environment. For example, marine crabs, move up and down the shoreline to maintain a constant environment in relation to tides (Begon et al. 1990). Conversely, some

planktonic algae may move between different habitats through a vertical migration, moving towards surface productive areas during the day to photosynthesize and migrating to deeper waters during the night to accumulate phosphorous and other nutrients (Salonen et al. 1984). Many species may move from one habitat to another multiple times within a 24-hour period. Many species of insectivorous bats display a bimodal distribution in their activity patterns (Erkert 1982). Resting during the day in protected roosts, these animals forage mainly at dusk and just prior to dawn, returning to the roost between forays.

In summary, migration whether on an hourly, daily or seasonal basis, is an important component in many species' lifestyles, which allows them to maintain growth and maximum survival.

## **1.2 Study Species Background**

The bull trout (*Salvelinus confluentus*) is a cold water char species native to Northwestern North America. There has been a noted decline in the stocks of many populations throughout its range over the past 25 years (Berry 1997). There are many reasons for the decline of the bull trout, including habitat alteration and destruction, increased competition with introduced fish species, and high levels of angling pressure (Berry 1997; Riehle et al. 1997; Post and Johnston 2001). Bull trout are currently regarded as a "vulnerable species" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Campbell 1990) and are recognized as a "species of special concern" by the American Fisheries Society and by Alberta Environmental Protection (Berry 1997).

Bull trout populations can generally be categorized into three different life-history categories: resident, fluvial and adfluvial (Northcote 1997; Post and Johnston 2001). The differences between each of these life-history types involve the extent of migration and habitat used by sub-adults and adults. Resident fish remain within the rearing stream for their entire life, whereas fluvial sub-adults migrate downstream into the mainstem river system and adfluvial sub-adults migrate into lakes. Migration out of cold water tributary streams into more productive riverine or lake habitat generally increases the growth rates of fluvial and adfluvial populations over residents.

Lower Kananaskis Lake, a 646 ha reservoir located in Peter Lougheed Provincial Park, Kananaskis Country, Alberta (50° 44' 31" N, 115° 14' 36" W) is approximately 150 km southwest of Calgary, Alberta (Figure 1.1). The lake supports a native adfluvial bull trout population that suffered severe declines in numbers due to overfishing (Stelfox 1997). In 1992, new initiatives were implemented to assist in the recovery of the population. These included the introduction of a catch-and-release fishery, bait ban and the closure to angling of Smith-Dorrien Creek, the spawning tributary. Since these changes, there has been a dramatic increase in the number of adult spawners that enter Smith-Dorrien Creek each fall to spawn, from 60 in 1992 (Stelfox 1997) to 1370 in 2000 (Mushens et al. 2003).

A detailed outline of the life history of the adfluvial bull trout in Lower Kananaskis Lake is shown in Figure 1.2. Migration 1 involves the first trophic migration that fry undertake from the spawning habitat to their first feeding habitat. Migrations 2 and 3 are coupled as diel movements. Juveniles carry out trophic migrations into feeding habitat at night, followed by a refuge migration into cover during the daytime. Refuge

has several purposes for juveniles in the creek, which may vary depending on the time of year. The first is as a velocity refuge while resting during the day. The second is as an interference or cannibalism refuge. In single species systems, juveniles have a lower predation risk compared to multi species systems, except in the fall when large adult conspecifics are also present in the rearing streams for spawning. Migration 4 is a second form of refuge migration that juveniles generally only undertake on a seasonal basis. This is the movement out of the rearing stream either in search of more productive habitat or as avoidance of interference or predation. Migrations 5 and 6 are once again daily movements of adults and sub-adults within the lake. This movement may not be as distinct as that displayed in juveniles. The final migration (7) involves mature adults that undertake a spawning migration into the shallow cold-water tributaries during the fall. They promptly return back to the lake once spawning is complete.

From this, the various migrations that an individual may undertake throughout its life can be seen. My thesis will focus on the diel movements, habitat use, and behaviour of juveniles in migrations 2 and 3 (Figure 1.2), and also the seasonal downstream migration into the lake of juveniles/sub-adults (migration 4).

### **1.3 Thesis Organization**

This thesis is divided into five chapters. The first chapter is designed to provide background on the bull trout of Lower Kananaskis Lake/Smith-Dorrien Creek and outline what aspects of their life-history were investigated. The following three chapters each focus on one specific part of the migration patterns and habitat use of juvenile bull trout: Chapter 2 – downstream migration of juvenile bull trout from Smith-Dorrien Creek into

Lower Kananaskis Lake, Chapter 3 – diel habitat use and movement within the stream, and Chapter 4 – the influence of adult bull trout on habitat use of juvenile bull trout during spawning. Chapter 5 is a short concluding chapter that summarizes results from all chapters.

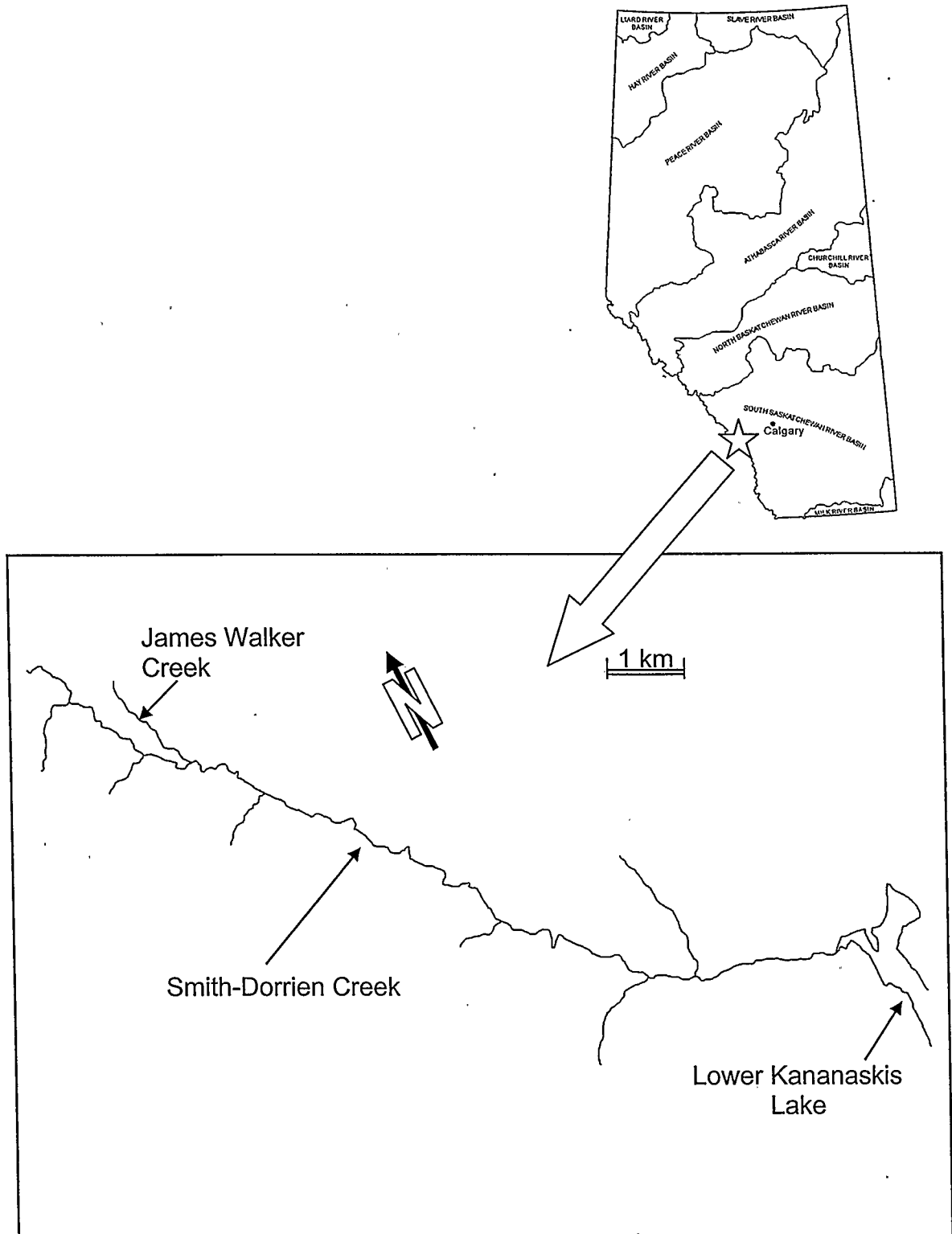


Figure 1.1 Map of Smith-Dorrien Creek and Lower Kananaskis Lake.



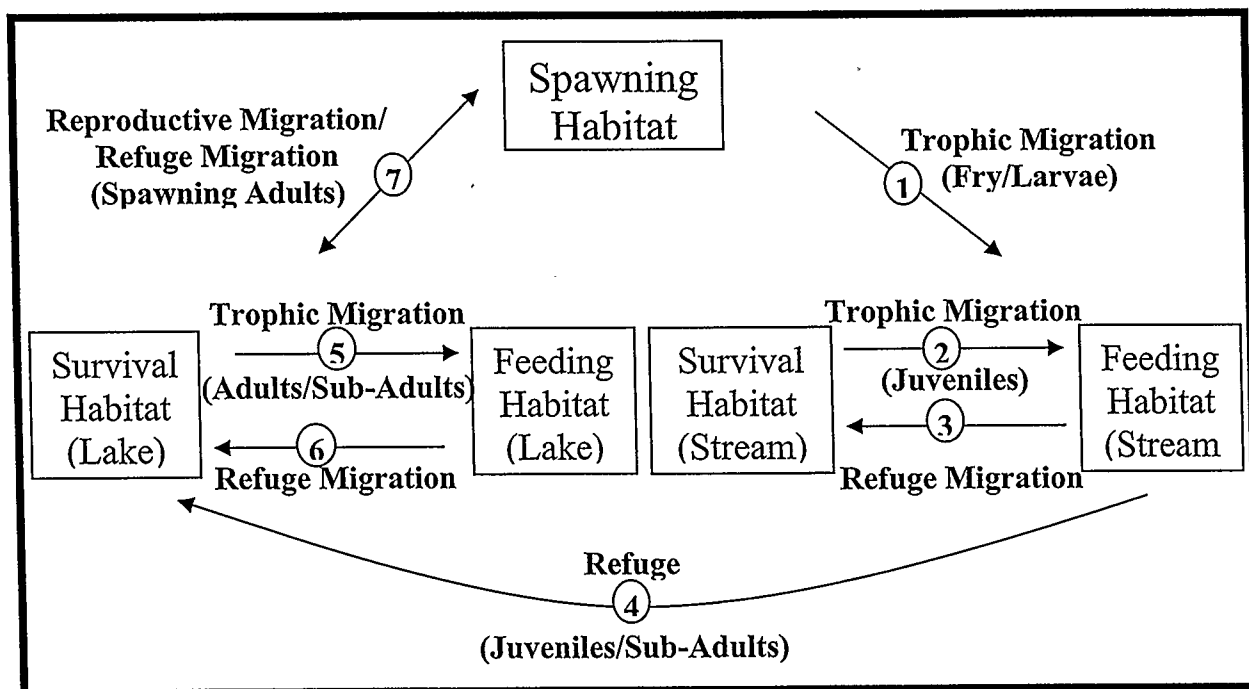


Figure 1.2 A generalized ontogenetic sequence (following numbers in circles) of an adfluvial bull trout population. (1) Larvae and fry undertake a trophic migration to their first feeding habitat. (2-3) Juveniles undertake daily migrations between feeding habitat and refuge habitat. (4) Juveniles/Sub-Adults undertake a migration out of the rearing stream into a lake system. (5-6) Adults/Sub-Adults in lake may undertake trophic migrations and return to survival habitat on a daily basis. (7) Adults undertake fall spawning migrations into spawning habitat in tributary streams and return to lake. Adapted from Northcote (1997).

## **Chapter 2 – Effects of environmental variables and inter-cohort interactions on adult and juvenile bull trout migration**

### **2.1 Introduction**

Migratory timing of fish, as well as the date of sexual maturation or spawning, is under partial genetic control (Quinn et al. 1997). Although genetics play a strong role in the seasonal timing of migration of fish (i.e. spring or fall spawners), especially in adults, the actual timing between years can vary considerably. Very often, migration is connected to the transition between life history stages, e.g. between hatching and the start of exogenous feeding, smoltification from a freshwater salmonid parr to a marine juvenile (Jonsson 1991). This migration is not necessarily consistent, with fish migrating out at various ages. Genetics may provide the instinctive drive for fish to undertake these movements, but environmental factors and social interactions may determine the specific timetable on a yearly basis. Water flow, water temperature and light are environmental variables that influence both when fish migrate, and the intensity of the migration (Northcote 1984). These factors can apply to both upstream and downstream migration.

Salmonids characteristically migrate between various life-history stages. Movements can be triggered by searches for critical habitat or food, or avoidance of adverse environmental conditions (Krebs 1978). The out-migration of juveniles from the rearing stream can be referred to as an ontogenetic shift. An individual must weigh the benefit of increased growth against the risk of increased predation, when moving into new habitat, or using a new niche (Anholt and Werner 1995). Increased movement

through either foraging or transit to new habitat usually increases encounter rates or detection by predators (Werner and Anholt 1993).

The effects of growth on migration are varied. Smoltification in various salmonids can occur at a higher rate for individuals with higher growth rates (Beckman et al. 1998; Metcalfe et al. 1998) or can be seen indirectly through larger fish moving downstream earlier (Bohlin et al. 1993; Bohlin et al. 1996). Smaller individuals have higher mass-specific metabolic rates and lower energy storage (Post 1990; Shuter and Post 1990). In light of the potential risks that face downstream migrants, larger or faster growing individuals may have an increased chance at survival to maturity. In contrast, salmonids with higher growth rates may be more likely to mature and forego smoltification for residency (Thorpe 1987; Jonsson 1991).

Jonsson (1991) discusses the importance of water flow for the river ascent of migratory fish. Either a certain discharge is required for the fish to move upstream past obstacles that may be impassable at low flows, or fish are unable to ascend before the discharge is below a threshold value. Discharge can be divided into two key factors that affect the ability of fish to undertake migrations: depth and velocity. Velocity and depth are inversely related to each other with respect to fish migration. Fish generally require either low velocities or high depth values.

Fish are poikilothermic animals and their activity is dependent on the temperature of the water. At low temperatures, they are less active than at higher temperatures, although higher temperatures incur higher energetic costs (Jonsson 1991). Therefore, it would be beneficial to fish to find a balance between discharge and temperature required to navigate the waterway while minimizing energy expenditure.

Temperature and flow may play a more limited role, or influence downstream migration through different means. Although some debate exists as to whether downstream migrations are active or passive (Jonsson 1991), it is most likely a combination of both. Compared to upstream migrants though, energetic expenditure is most likely less of a concern to downstream migrants. The passive component may be that water flow is the vector that displaces the fish downstream. The active component of downstream migration may involve choosing when to move into the current when initiating migration (Naesje et al. 1986, Solomon 1978, Hansen and Jonsson 1985), or the active avoidance of obstacles (Hansen and Jonsson 1985) or even predators.

Information on the environmental requirements of upstream-migrating bull trout is limited. McPhail and Murray (1979) is one of the few reports available that discusses the relationship of migration to temperature and flow. The upstream movement of Dolly Varden (*Salvelinus malma*) in Upper Arrow Lakes, B.C., occurs in early August during the period of highest water temperatures (10.0 – 12.0 °C) and lowest water levels (McPhail and Murray 1979). This evidence corroborates the hypothesis that the upstream migration occurs at a time that minimizes effort and maximizes activity levels. Until only recently (1978), bull trout were commonly known as Dolly Varden (Cavender 1978), being virtually identical to the untrained eye and both displaying similar life history traits. It is reasonable to assume that bull trout may have similar migratory tactics to Dolly Varden.

Lower Kananaskis Lake provides the potential for increased growth for juveniles compared to Smith-Dorrien Creek. Lower Kananaskis Lake contains a much broader

food base and annual growth rates of juveniles that move into the lake increase by a factor of two (Mushens et al. 2003).

The goal of this chapter is to investigate what, how and why environmental factors affect the movement of bull trout. The questions addressed in this chapter include:

- (1) what environmental variables influence the upstream spawning migration of adult bull trout?
- (2) how do environmental variables influence the downstream migration of juvenile bull trout?
- (3) do juvenile migrants exhibit growth rates different from the rest of the population?
- (4) does the timing of upstream movement of adults influence the timing of downstream movement of juveniles?

## 2.2 Methods

### 2.2.1 Study Site

Smith-Dorrien Creek and Lower Kananaskis Lake are situated in the Eastern slopes of the Rocky Mountains approximately 150 km southwest of Calgary, Alberta. The 646 ha reservoir supports populations of rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*O. clarki*), bull trout, longnose sucker (*Catostomus catostomus*), white sucker (*C. commersoni*) and various cyprinids. Smith-Dorrien Creek is 13 km long and flows into Lower Kananaskis Lake from the northwest (Figure 2.1). It is a coldwater stream (mean daily summer temperature = 5.2 °C) with peak flows occurring from mid-

June to early July as the winter snowpack melts (Mushens et al. 2003). Adfluvial bull trout of Lower Kananaskis Lake use Smith-Dorrien Creek for spawning, and juvenile bull trout spend up to 4-years rearing in the creek before migrating to Lower Kananaskis Lake to mature (Stelfox 1997). In addition to the adfluvial population that uses Smith-Dorrien Creek, a small resident population of bull trout also inhabits the creek. Other fish species are absent from Smith-Dorrien Creek except young-of-year suckers (*Catostomus* spp.) in the lower 500 m of the creek, and the occasional large rainbow trout or cutthroat trout that has moved into the creek from the lake. Both rainbow and cutthroat trout are intermittently stocked into Lower Kananaskis Lake (Stelfox 1997).

### **2.2.2 Migration**

I determined timing of upstream migration of adults and the downstream migration of juveniles each year using a fish fence and trap (Figure 2.2). The fence consisted of sections of 5.1-cm aluminium-angle bolted together with upright supports to create a frame. These sections were supported by wooden A-frame supports bolted together to form a continuous linear fence. Each section of frame measured 122-cm wide by 152-cm high and consisted of three horizontal pieces of aluminium-angle with 45 holes (1.4-cm diameter) evenly spaced to vertically fit 203-cm long by 1.3-cm diameter aluminium rods. The gaps between adjacent rods were each 1.4 cm.

Fish were captured in traps measuring 122 cm high by 122 cm wide by 183 cm long and had funnels that were 122 cm wide and 92 cm tall at the entrance, tapering to 32 cm in diameter and measured 183 cm in length. These funnels were suspended in the



middle of the water column by water pressure or by a rope tied to the upstream end of the trap. The traps were constructed of an aluminium-angle frame covered with either hardware-cloth (1996) or Durethene plastic (1997 to 2000) screen mesh (0.6 cm by 0.6 cm), and had locking plywood lids.

To ensure that all upstream migrants were captured, an incline plane trap was also installed directly downstream of the trap. In 1996 the trap was constructed from 120 cm by 15 m hardware cloth with 2.5 cm by 2.5 cm mesh. The 47.5 cm base was covered with landscaping cloth and then secured to the substrate with sandbags. The remaining 72.5 cm was angled upstream with the leading edge secured with notched metal fence posts at a depth of 12 cm to 15 cm below the surface. Adjustable to changes in water level, this allowed fish to move upstream over the incline, but prevented most of them from returning downstream, facilitating easy capture for tagging. From 1997 through 2000, Durethene plastic mesh (3.8 cm by 3.8 cm) was used as it was determined to be less abrasive than wire mesh and appeared to reduce Floy tag loss.

Traps were checked each morning on a daily basis from late-July to mid-October, 1996 to 2000. Fish were measured, weighed and tagged before being released.

### **2.2.3 Temperature**

Temperature was measured in the creek throughout the year using an Onset optic stowaway thermograph located 100 m upstream from the fish fence. This device recorded temperatures every 35 minutes. Mean daily temperature, mean weekly temperature and maximum daily temperature were used for analysis. The weighted mean

temperature (Quinn et al. 1997) was calculated for adults moving upstream in categories of: 0-5%, 6-25%, 26-50%, 51-75%, and 76-95% of the total spawning migration each year. Instead of calculating the mean temperature over the period that a particular proportion of fish moved upstream, the weighted mean temperature takes into consideration the number of adults that moved upstream on a particular day.

#### **2.2.4 Discharge**

Depth was measured on a daily basis using a staff gauge situated in the creek upstream of the trap. Water depth on the staff gauge (m) was calibrated with discharge readings taken at various water levels throughout the summer. Water velocity ( $\text{m}\cdot\text{s}^{-1}$ ) was measured at one-metre intervals across the creek at a predetermined location using a Marsh-McBirney Flo-Mate model 2000 velocity meter. Discharge ( $\text{m}^3\cdot\text{s}^{-1}$ ) was calculated for each one metre section: water velocity ( $\text{m}\cdot\text{s}^{-1}$ ) \* depth at measurement (m) \* width of segment (1 m), and then summed across the creek. These discharge readings were then regressed against the staff gauge readings, allowing determination of discharge throughout the season using only a simple measurement of water depth. As with temperature data, the weighted mean discharge was calculated for the time period when adults were moving upstream each year.

#### **2.2.5 Moon Intensity**

Measurements of moon intensity and duration for each night were calculated using the software Moonrise 3.5 (Bruce Sidell, <http://www.iserv.net/~bsidell/>)

moonrise.htm). This software provided the times of moon rise and set, morning and evening twilight and moon intensity for the latitude specified ( $50^{\circ} 44' 31''$  N,  $115^{\circ} 14' 36''$  W). Moon intensity was measured in percent of full moon. Therefore, 100% would represent a full moon and 0%, a new moon. Moon duration was calculated as the amount of time that the moon was above the horizon each night between evening and morning twilight. Unfortunately, instruments were not available to measure actual light intensity each night, and actual weather conditions (i.e. rain and cloud cover) were not taken into consideration.

#### **2.2.6 Growth Rates**

Growth rates of juveniles were determined by recapturing juveniles in the creek throughout the season. In 1998 and 1999, two 1.5 km sections of creek were surveyed for juvenile bull trout. Sampling occurred approximately every three weeks from May through October in both years. Fish were captured by night netting, a technique adapted from Bonneau et al. (1996). This consisted of walking upstream, illuminating the water with halogen dive lights until an individual fish was observed. Once located, a dip net (0.6 mm dark-green mesh with an opening of 0.2 X 0.6 m) was placed about 0.2 m downstream of the fish. The fish was then coaxed into the dip net from upstream using a rigid nylon sieve attached to a pole. Each bull trout was mildly anaesthetized (tricaine methane sulfonate – MS 222), after which the fish was measured (nearest 1 mm) and then marked using Passive Integrated Transponder (PIT) tags (Prentice et al. 1990). Each tag, measuring 12 mm long by 2 mm in diameter, was inserted into the body cavity using a

14-gauge hypodermic needle modified with a stainless steel ramrod attached to the plunger. Tags were inserted approximately three quarters of the way between the pectoral and pelvic fins and just to the right side of the ventral line. The needle pierced the skin after which the tag was inserted by depressing the plunger. The minimum size of fish tagged was 75 mm fork length (FL).

Weekly mean growth rates were calculated for juveniles that were recaptured throughout the season. Measurements were used from fish that were recaptured within a two to eight week period. Growth may not be easily determined on fish captured within less than a two week period due to inaccuracy in measuring techniques, and seasonal changes in growth would be obscured in periods longer than eight weeks. The mean growth for each two week period was calculated from all fish measured within that time period. The residual growth rate for each fish was calculated by subtracting its growth rate from the mean growth rate. Due to variability in the variance between time periods, each value was standardized by dividing the residual growth rate by the standard deviation. The standard deviation for each period after standardization had a value of one. Without standardization, residual growth rates would be biased towards fish whose numerical difference was large, but may have experienced low growth relative to others within that time period. In contrast, a fish caught in a month with low variance may have an extremely high growth rate relative to others, but the numerical difference may be low.

To determine whether juveniles that migrated out of Smith-Dorrien Creek had higher residual growth rates than the rest of the population, I used logistic regression analysis. I regressed the binary dependent-variable migrate (whether the individual migrated out of the creek or not), against the independent variable of the standardized

residual growth rate. The effect of growth rate on the probability of migration was tested using the LOGIT function in SYSTAT (Wilkinson et al. 1992). The resulting logistic model predicts the probability of an individual migrating downstream or not based on the value of the standardized residual growth rate according to the equation

$$\text{Pr} = \frac{1}{1 + e^{-(a+bx)}} \quad (2.1)$$

where Pr is the probability that an individual will migrate,  $a$  is a constant and  $b$  is the slope parameter for the independent variable. Results from the logistic regression were tested for significance with the log likelihood ratio test. The difference between the negative log-likelihoods of the full model and a nested model with one parameter removed provided the value for the likelihood ratio test (Hilborn and Mangel 1997). Twice the likelihood ratio follows a chi-square distribution with one degree of freedom (Hilborn and Mangel 1997), and therefore this value must be  $> 3.84$  for the parameter to significantly contribute to the model with  $\alpha < 0.05$  (Paul 2000).

I compared the size of age-2 and age-3 bull trout that migrated downstream to their counterparts in the creek using ANOVA to determine whether individuals that migrated downstream were larger than those in the creek within an age class. To do this, I had to assign each fish to an age class. Using age data from otoliths of mortalities collected in Smith-Dorrien Creek from 1997 to 1999, I regressed fork length of fish in each age class over time (Figure 2.3). I had data from May through October for age-1 ( $n=24$ ) and age-2 ( $n=70$ ) fish and from the end of July through October for age-3 fish ( $n=39$ ). The slopes for regressions for age-1 and age-2 fish were homogenous, but there were not enough data over time for age-3 fish to develop a significant regression. To use

age-3 data, I assumed that the slope of growth over time for age-3 fish was equal to that of age-1 and age-2 fish, as supported by Paul (2000). Assuming that fork lengths in an age class are normally distributed, the mean and standard deviation derived from the regressions were applied to a likelihood model outlined in Paul (2000). The probability of belonging to each age class was calculated and the age was assigned to the age class with the highest probability.

### **2.2.7 Inter-Cohort interactions**

Time series analysis was conducted on the upstream migration of adults and the downstream migrational movement of juveniles. Weekly movements of both adults and juveniles were compared using cross-correlation function in SYSTAT (CCF function, Wilkinson et al. 1992). Cross-correlation plots identify relationships and delays between two time series (Wilkinson et al. 1992).

## **2.3 Results**

### **2.3.1 Adult Upstream Migration**

#### **Timing**

The timing of upstream migration of adults and downstream migration of juveniles varied over the five-year study (Figure 2.4). Initiation of migration began over a two week period from the end of July (1998) to 12 August (1996). Based on the time by which at least 5% of the adults had moved upstream, initiation of migration varied between years from 1 to 20 August (Figure 2.5). In most years, 5% had moved upstream



by 12 August. Likewise, the completion of upstream migration also varied over the period by approximately three weeks, from 5 to 26 September. The upstream migration is also multimodal in many years. The large initial influx of adults has been attributed to the movement of primarily first-time spawners (Mushens et al. 2003), after which repeat spawners begin to move upstream. Variation in the timing of migration between years suggests that various environmental variables may play a key role.

### **Temperature, Discharge and Moon Intensity**

The general relationship between discharge and temperature can be described as a cyclical pattern throughout the season (Figure 2.6). Throughout the winter, most of the water supply is contained within the snow pack, leading to low flows in combination with low temperatures. As spring approaches, photoperiod increases leading to increasing stream temperatures, but still minimal flows due to water contained in the snow pack. With further increasing temperatures, the snow pack begins to melt and flows increase rapidly during May and June and runoff occurs. During this time, although the water volume increases, the mediating temperature of the melted snow maintains a fairly constant temperature at around 5°C. Once the majority of runoff has occurred, stream flows begin to decline and temperatures continue to rise to the seasonal maximum in early August, after which temperatures follow a steady decline corresponding with declining photoperiod. Mean daily temperature from June 1 to September 30 1996 - 2000, was 5.6°C (range 5.0 – 6.7). Temperatures in Smith-Dorrien Creek can fluctuate as much as 7.2°C (range 6.4 – 7.8) within a 24 hour period.

In all years, upstream adult migration appears to start when discharge is decreasing and stream temperature has peaked (Figure 2.7). Discharge may play an important cue in initiation, with virtually no fish moving at discharges higher than  $3.5 \text{ m}^3 \cdot \text{s}^{-1}$ . A restriction in the channel width at the site of a rapid at the confluence of the stream and the lake downstream of the trap may create prohibitive velocities for bull trout at discharges above  $3.5 \text{ m}^3 \cdot \text{s}^{-1}$ . Actual temperature values did not appear to strongly affect the initiation (first 5%) of migration, as mean temperatures varied as much as  $1.4^\circ\text{C}$  between years ( $6.1^\circ\text{C}$  in 1999 -  $7.5^\circ\text{C}$  in 1998). The number of adults that moved upstream within a day was positively related to positive changes in water temperature (Figure 2.8). Larger numbers of individuals moved upstream on nights where that day's maximum daily temperature was higher than that in previous days. In cool years such as 1999, upstream migration was highest during days when temperatures exceeded  $8^\circ\text{C}$ , whereas in 1998, limited migration occurred at temperatures around  $8^\circ\text{C}$  possibly because it was at the low end of the scale in terms of relative temperature. Within the temperature ranges observed in Smith-Dorrien Creek, bull trout do not appear to prefer a particular temperature when migrating upstream, but instead prefer high positive temperature changes within a season.

Initiation of migration took place in various years both during periods of high and low moon intensity and duration (Figure 2.9). It is important to note that these results are determined from the estimated moon intensity and duration for the latitude of Smith-Dorrien Creek. It does not take into consideration local weather conditions and cloud cover. It is unknown whether cloud cover during times of expected high moon intensity affected migration. Migration was common during times of low moon intensity.

### **2.3.2 Juvenile Downstream Migration**

#### **Timing**

The start of downstream migration of age-2 and age-3 juveniles varied between years from Aug 6 to Aug 26 (Figure 2.4). Juveniles were not common in the downstream trap before the upstream migration of adults. In most years the trap was installed and operational by late July, but in 1993 the trap was operational from May to October (Stelfox 1997). In 1993, only 11 (4%) of 288 juveniles were caught from May through July (Stelfox 1997), confirming that only limited migration occurs before August. Numbers migrating downstream each year also fluctuated, suggesting differences in the size of individual cohorts.

#### **Temperature and Discharge**

It was not possible to pinpoint key temperature or discharge levels at which juveniles began to migrate downstream because of the lack of knowledge of the position of juveniles within the stream. Juveniles at various locations upstream of the trap would have different transit times to the mouth of the stream. Therefore, a juvenile located 10 km upstream of the trap may have taken a week to move downstream, whereas a juvenile located 1 km upstream of the trap may have initiated downstream migration the previous night. It was not possible to determine how far an individual juvenile had traveled, and therefore impossible to determine what combination of environmental variables were present at the initiation of downstream migration. In contrast to adults that may key in to variables such as temperature and discharge to minimize energy expenditure during the

spawning migration, juveniles are undertaking an ontogenetic shift, which can often be attributed to changes in growth.

## Growth

Weekly growth rates of juveniles displayed a positive linear relationship to stream temperature throughout the season in both 1998 and 1999 (1998:  $df = 19$ ,  $t = 7.09$ ,  $P < 0.001$ ; 1999:  $df = 22$ ,  $t = 4.04$ ,  $P < 0.001$ ). Juveniles in 1998 experienced high growth rates that peaked in late July and declined with falling temperatures in August and September (Figure 2.10). Temperatures in 1999 did not display such a distinct peak as in 1998, but instead increased gradually from around 4°C in late May to a peak of around 6°C by late August. Likewise, growth rates in 1999 were more consistent throughout the season with a short peak at the beginning of July. Although growth rates in 1998 (mean 1.8 mm·week<sup>-1</sup>), were higher than in 1999 (mean 1.5 mm·week<sup>-1</sup>), 1999 growth rates were much less variable and not significantly different from 1998 ( $F = 1.13$ ,  $df = 25$ ,  $P = 0.30$ ).

Logistic regression analysis of the occurrence of a juvenile migrating downstream as a function of their standardized residual growth rate revealed that juveniles that experienced higher growth rates throughout the summer were more likely to migrate downstream. In 1999 juveniles that experienced higher growth rates exhibited a significantly higher probability of migrating downstream in the fall, and 1998 results were only marginally non-significant (Table 2.1; Figure 2.11). Due to low numbers of downstream migrants with measured growth rates for each year, the standardized data for 1998 and 1999 were combined. Results show a significant positive relationship between

standardized growth rate deviation and the probability of migrating downstream. Growth rates in 1998 showed a weak but significant positive relationship to size ( $F = 18.33$ ,  $df = 177$ ,  $P < 0.0001$ ; Figure 2.12). In 1999, growth rates were symmetrical across size ( $F = 1.22$ ,  $df = 142$ ,  $P = 0.27$ ).

The majority of bull trout that migrated downstream were age-2 or age-3. A size-frequency distribution of juveniles caught in Smith-Dorrien Creek in both 1998 and 1999 according to age was developed (Figure 2.13). In both years, and for age-2 and age-3, fish that migrated downstream were significantly larger than individuals within their age class that remained within the stream (Table 2.2).

### **Inter-Cohort Interactions**

The downstream movement of juveniles consistently occurred after initiation of the upstream spawning migration of adults. Cross-correlation plots of the weekly movement of adults and juveniles show that the downstream migration of juveniles occurred one to two weeks after the upstream migration of adults (Figure 2.14). In three of the five years (1996, 1997 and 2000), the results were statistically significant and the remaining years (1998 and 1999) showed the same general pattern.

## **2.4 Discussion**

### **2.4.1 Adults**

The initiation of the spawning migration of adult bull trout in Lower Kananaskis Lake can occur over a two week window from the end of July to mid-August each year.

Variation in the timing of the upstream movement of adult bull trout appears to be associated with positive changes in temperature and declining discharge (specifically flow). Actual temperature values did not appear to affect the initiation of upstream migration, with variations in temperature at the start of migration observed between years. In each year, more adult bull trout moved upstream on days (nights) with a positive temperature change from previous days. Upstream migration each year did not start until stream discharge dropped below  $3.5 \text{ m}^3 \cdot \text{s}^{-1}$ , which is likely associated with restrictive velocities at a rapid located at the confluence of the lake and stream. There was no relationship between moon phase and bull trout migration.

The timing of adult movement out of the lake or reservoir can vary widely between populations. Adfluvial populations such as that in Flathead Lake, Montana, move out of the reservoir during April and May (Fraley and Shepard 1989), and those in Lake Billy Chinook, Oregon, in May and June (Riehle et al. 1997). Individuals in the Flathead Lake population may migrate upstream over 250 km to reach suitable spawning habitat in some North Fork tributaries in British Columbia (Fraley and Shepard 1989). These fish may spend the entire summer slowly moving upstream to such locations in stages. The Lower Kananaskis Lake bull trout population has a relatively small distance to migrate to their spawning grounds (approx. 13 km). In all cases though, adults are reported to enter into their respective spawning tributary in late July or August (Fraley and Shepard 1989; Riehle et al. 1997; Stelfox 1997).

Few studies provide detailed information on both discharge and temperature to be able to assess the relationship between these environmental variables and the migration of bull trout. McPhail and Murray (1979) provide observations that support the relationship

of adult Dolly Varden moving upstream during the time when flows are low or declining and stream temperatures are high but declining. This relationship is important to such fish from an energetic perspective. In the coldwater systems that bull trout inhabit, the initiation of upstream migration during low flows minimizes energy expenditure, while high temperatures ensure that activity levels are high. At higher temperatures activity levels are higher, allowing faster reactions to predator threats or in attaining high speeds to negotiate high velocity stream flows (Webb 1978). Over temperature ranges from 5 to 25°C, in 5°C increments, Webb (1978) found that acceleration performance was higher and response latency lower at higher temperatures in rainbow trout (*Oncorhynchus mykiss*). Of course being coldwater specialists (Fraley and Shepard 1989; Saffel and Scarnecchia 1995; Rieman and McIntyre 1995), the activity range for bull trout is much lower than for rainbow trout. Bull trout were rarely found in tributary streams of Lake Pend Oreille, where the maximum temperature exceeded 15°C (Saffel and Scarnecchia 1995), and were not found in streams in the Flathead drainage, where maximum temperatures exceeded 18°C and were most abundant where temperatures were less than 13°C (Shepard et al. 1984).

Although adult bull trout migration was best related to the maximum daily temperature, it is not these temperatures that the fish will encounter at the time of migration. Bull trout migration occurs primarily at night. Although nighttime migration provides protection from predators (Jonsson 1991), it may be a hindrance with respect to activity levels. In such a cold-water environment, activity levels can be affected by declining temperatures at night. Therefore, high temperatures during the daytime may provide an indication of the ambient stream temperature during the upcoming night.

#### 2.4.2 Juveniles

Each year age-2 and age-3 bull trout undertake an ontogenetic shift as they migrate downstream from the rearing stream into a lake or larger river to grow into adults. The initiation of downstream migration of juvenile bull trout from Smith-Dorrien Creek into Lower Kananaskis Lake varied over a three week period beginning at the start of August. Juveniles that migrated downstream had higher growth rates and were larger than that of juveniles in their respective age class still residing in Smith-Dorrien Creek. A positive correlation was found between the downstream migration of juveniles and the upstream migration of adults. The downstream migration of juveniles consistently occurred one to two weeks after the upstream migration of adults had started, suggesting that adults may influence the movement of juveniles in Smith-Dorrien Creek.

There is evidence that migratory behaviour can be influenced by growth (McCart 1997), although both high and low growth rates have been noted to be responsible. Both large and small spring chinook salmon (*Oncorhynchus tshawytscha*) smolts exposed to conditions producing higher growth rates were more likely to migrate downstream than fish with lower growth rates (Beckman et al. 1998). Conversely, in 15 species of fish, five of them *Salvelinus* sp. (but not *S. confluentus*), those individuals which remained in the stream as residents instead of smolting were the fastest-growing juveniles in their year classes (Thorpe 1987).

If declining growth rates play a key factor in the downstream migration of juveniles, why did juveniles move downstream earlier in 1998 than in 1999? Growth rates and temperature were much higher in 1998 than that in 1999 at the initiation of migration. What factors occurred earlier in 1998 than in other years that made juveniles



move downstream earlier? Low flows and warm temperatures made 1998 an extremely favourable year. Also, the size and growth rates of juveniles that did migrate downstream do not support the idea that fish with higher growth rates remain in the stream.

The hypothesis that food limitation forces larger individuals to migrate downstream is not well supported. In fact, Paul (2000) showed that growth rates within enclosures in Smith-Dorrien Creek were constant across body size. Even in high density, low growth enclosures, size asymmetries in growth were not present. Actual in-stream measurements of growth rate were not size dependent in 1999, with a weak but significant positive relationship in 1998. My logistic regression analysis has shown that juvenile bull trout within Smith-Dorrien Creek appear to initiate downstream migration on the basis of higher growth rates. This is also supported by the fact that juveniles that moved downstream were larger individuals from within their cohort. These larger individuals would have had to have experienced higher growth rates to achieve the larger size. Therefore, an alternate explanation for the early downstream migration of juveniles in 1998 is that the timing of downstream migration is controlled by size or growth rate, similar to that found in the control of the timing of smoltification in chinook salmon. Large and small juvenile chinook salmon that had been raised in a warmwater environment (higher growth rate), were more likely to smolt than large and small individuals raised in a coldwater treatment (low growth rate; Beckman et al. 1998).

Why would growth rate be an important factor in determining downstream migration of juveniles? The movement of juveniles downstream into Lower Kananaskis Lake can be considered an ontogenetic shift. Migration has been suggested to be an active fitness-promoting strategy that may entail size-dependent costs (Bohlin et al.

1996). Many important factors scale with body size, e.g. predation risk and susceptibility to physical factors, which either influence fitness directly or affect patterns of resource use (Werner and Gilliam 1984). For many taxa, there is a selective premium for fast growth early in the life history. An increased growth rate reduces the time spent in smaller, more vulnerable size classes and thereby minimizes the overall risk of mortality. It can also increase the range of prey types and the mean prey size (Werner and Gilliam 1984). Smaller individuals have higher mass-specific metabolic rates and lower energy storage, and therefore suffer more than larger individuals during periods of resource scarcity (Post 1990; Shuter and Post 1990). The benefits of ontogenetic shifts are often quantified by the tradeoff between the relative increases in both growth and mortality rates (Werner and Gilliam 1984; Landry et al. 1999; Post et al. 1999).

Predation risk for juvenile bull trout in Lower Kananaskis Lake will most likely be higher than that experienced in Smith-Dorrien Creek due to an increased risk of encountering large piscivorous conspecifics. The timing of their fall migration is advantageous as predation risk in the lake will inevitably be reduced as the majority of adult bull trout spend August through September spawning in Smith-Dorrien Creek. Of course, the downstream migration may be increasingly hazardous as juveniles encounter adults moving upstream. Each year the downstream migration of juveniles occurs one to two weeks after the upstream migration of adults. Could the presence of adults affect the initiation of downstream migration? This one to two week lag would account for the transit time for adults to move upstream and for the juveniles to migrate downstream. The predation risk of migratory adults on juveniles in the creek was not directly measured due to the influence it may have on the spawning behaviour, but some anecdotal evidence

provides insight into the potential for cannibalism during the upstream migration of adults and the downstream migration of juveniles. Adult spawners consumed 2 (9.5%) of 21 juvenile bull trout that were implanted with radio-telemetry tags in 1999. Resident adults, generally over 350 mm in length that have been captured during night-netting sample periods between August and October, have also provided evidence of cannibalism. Of 22 residents captured during 1998 and 1999, 4 (18%) had consumed juveniles that had PIT tags implanted. This can be used as a very conservative estimate of predation risk of large bodied adults on juveniles within Smith-Dorrien Creek. The total number of untagged juveniles that may have been cannibalized is unknown. It is possible that during August and September each year, predation risk is actually lower in the lake than it is in Smith-Dorrien Creek.

How do juvenile bull trout benefit from moving into Lower Kananaskis Lake? The average annual growth rate for juvenile bull trout in Smith-Dorrien Creek is  $44.0 \text{ mm}\cdot\text{yr}^{-1}$ , whereas in Lower Kananaskis Lake, the average annual growth rate for juveniles doubles to  $96.1 \text{ mm}\cdot\text{yr}^{-1}$  (Mushens et al. 2003). The downstream migration is comprised of primarily age-2 and age-3 fish. The age-2 fish benefit from moving downstream at a younger age by maturing on average one year younger than age-3 migrants (Mushens et al. 2003). Data also indicate that there is no difference in the survival rate between age-2 and age-3 juvenile bull trout from the time of migration to maturity. The probability of a juvenile bull trout that migrated downstream in 1995 surviving to maturity was 0.35 (Mushens et al. 2003).

In summary, the upstream spawning migration of adult bull trout in Lower Kananaskis Lake/Smith-Dorrien Creek varies seasonally and key factors that affect

timing were changes in stream temperature and stream flow. Bull trout densities were highest during times when an increase in daily temperature had occurred. Although actual velocities at the first high velocity habitat unit in Smith-Dorrien Creek could not be measured, the discharge value of  $3.5 \text{ m}^3 \cdot \text{s}^{-1}$  likely corresponds to the upper threshold of stream flow that adult bull trout choose to navigate. Sampling design prevented the assessment of environmental factors on the downstream migration of juvenile bull trout. Knowledge of environmental factors associated with the time and location of juvenile bull trout in the stream when they begin to move downstream would be required. Bull trout that move downstream to the lake were larger and had higher growth rates than those of conspecifics that remained in the stream. Larger, faster growing fish may take greater risks to benefit from higher growth rates, earlier maturity and a better probability of survival in the long run. The strong correlation between the timing of the upstream migration of spawning adults and the downstream migration of juveniles suggests that stream flow and temperature may determine migratory timing in both of these life-history stages, but also that adults may influence the movement and behaviour of juveniles in the creek.

Table 2.1 Logistic regression models relating the chance of a juvenile migrating downstream as a function of its mean standardized growth rate deviation (Growth) or a constant. Twice the difference in negative log-likelihoods between the full model (constant + Growth) and either of the two simpler models, with one parameter removed, follow a chi-square distribution with one degree of freedom. A significant chi-square value (i.e.  $P < 0.05$ ) indicates the removed parameter significantly contributed to the model.

Year	Model	Estimated Parameter values	Negative Log- Likelihood	Chi Square Value	P
1998	Constant + Growth	Constant = -2.22 Growth = 0.75	-32.63	--	--
	Constant (Growth removed)	Constant = -2.08	-34.53	3.81	0.051
	Growth (Constant removed)	Growth = 0.31	-67.89	70.53	< 0.001
1999	Constant + Growth	Constant = -2.05 Growth = 1.26	-33.80	--	--
	Constant (Growth removed)	Constant = -1.76	-39.72	11.84	0.001
	Growth (Constant removed)	Growth = 0.73	-61.65	55.70	< 0.001
Combined	Constant + Growth	Constant = -2.13 Growth = 1.00	-67.20	--	--
	Constant (Growth removed)	Constant = -1.91	-74.54	14.68	< 0.0001
	Growth (Constant removed)	Growth = 0.53	-130.17	125.94	< 0.0001

Table 2.2 Analysis of variance (ANOVA) of size between migrant and instream bull trout for each age class (age-2 and age-3), and both years (1998 and 1999).

Source		Sum of Squares	DF	Mean Square	F	P
1998 Age-2	Between Groups	7800.9	1	7800.9	62.24	< 0.0001
	Within Groups	37101.1	296	125.3		
	Total	44902	297			
1998 Age-3	Between Groups	649.8	1	649.8	5.61	0.018
	Within Groups	35674.5	308	115.8		
	Total	36324	309			
1999 Age-2	Between Groups	24914.1	1	24914.1	216.6	< 0.0001
	Within Groups	40948.8	356	115.0		
	Total	65863	357			
1999 Age-3	Between Groups	2020.7	1	2020.7	19.84	< 0.0001
	Within Groups	19247.3	189	101.7		
	Total	21268	190			

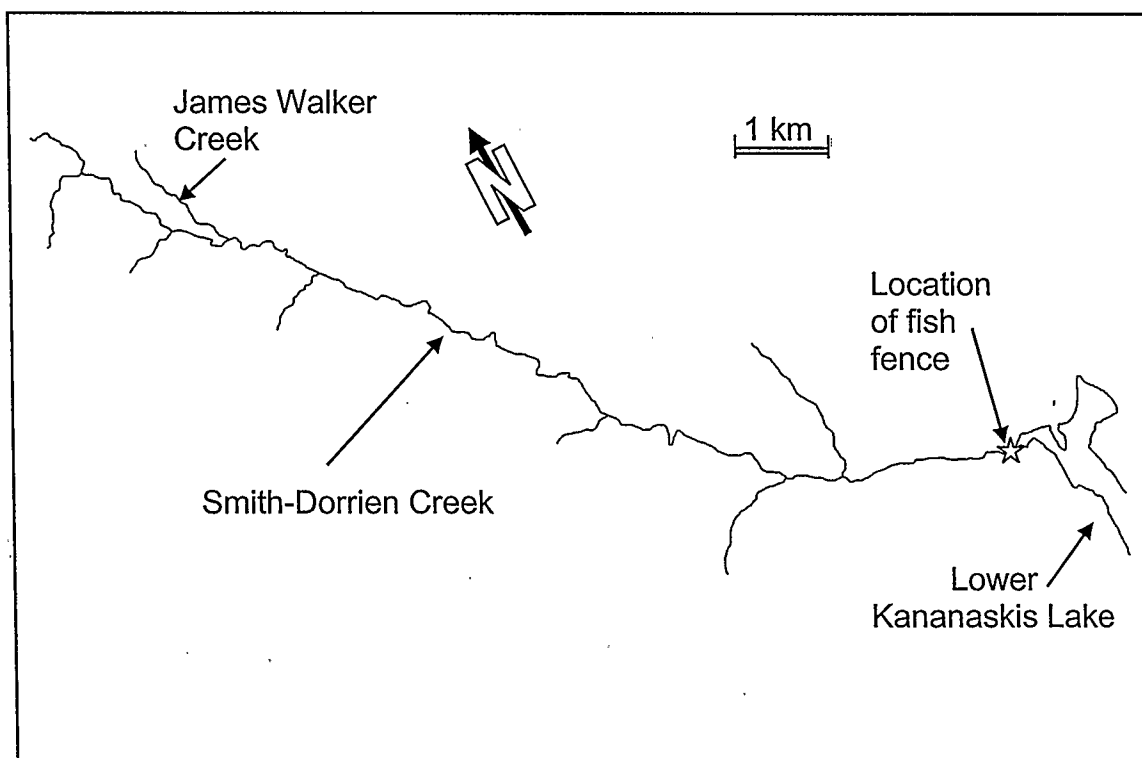


Figure 2.1 Map of Smith-Dorrien Creek indicating the location of the fish fence.

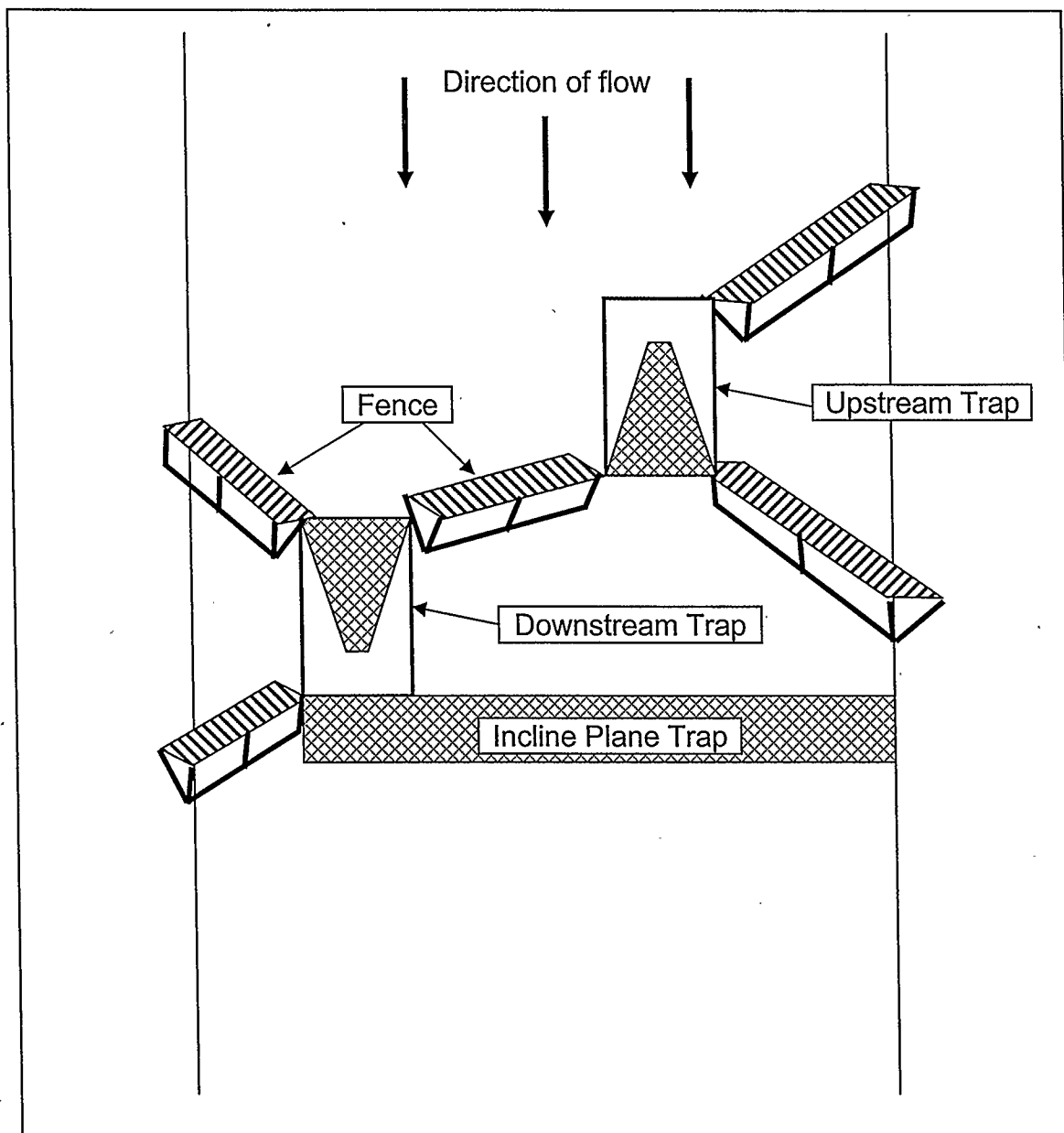


Figure 2.2 Schematic of fish fence and trap on Smith-Dorrien Creek.



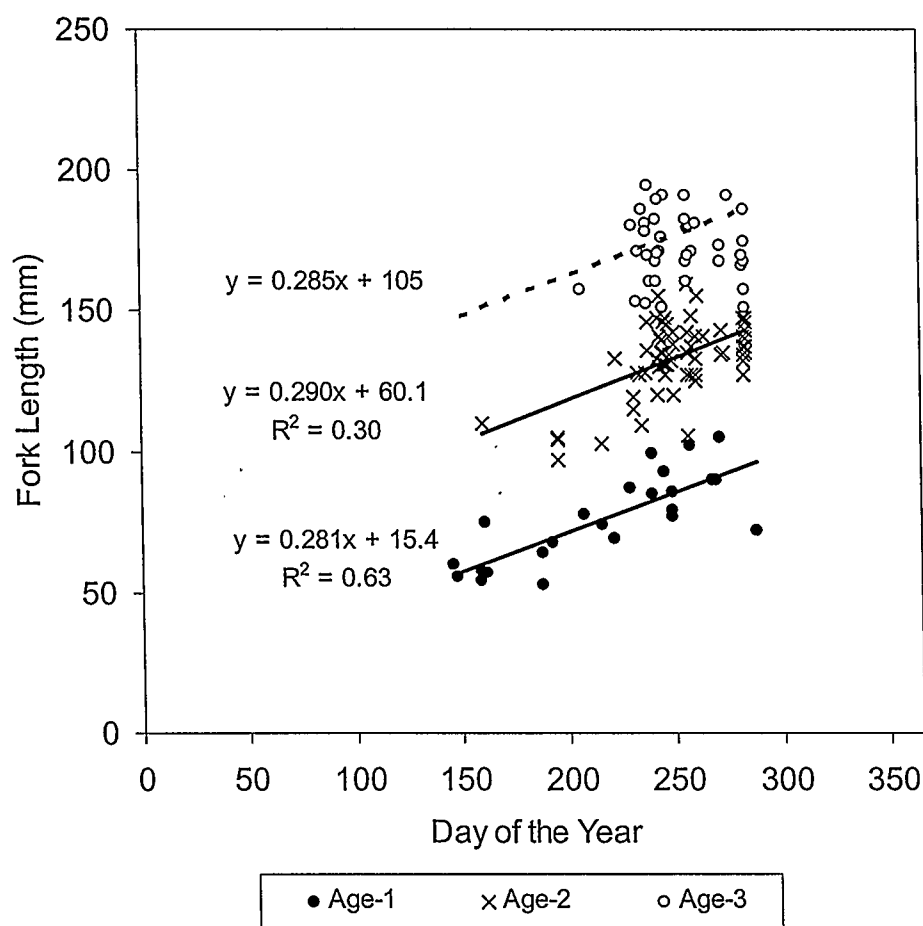


Figure 2.3 Plot of fork length of juvenile bull trout aged from otoliths against day of the year when sampled. The slope in the regression equation for each age class corresponds to the daily growth rate. The regression line and equation for age-3 fish is estimated from the average of the slopes of age-1 and age-2 fish.

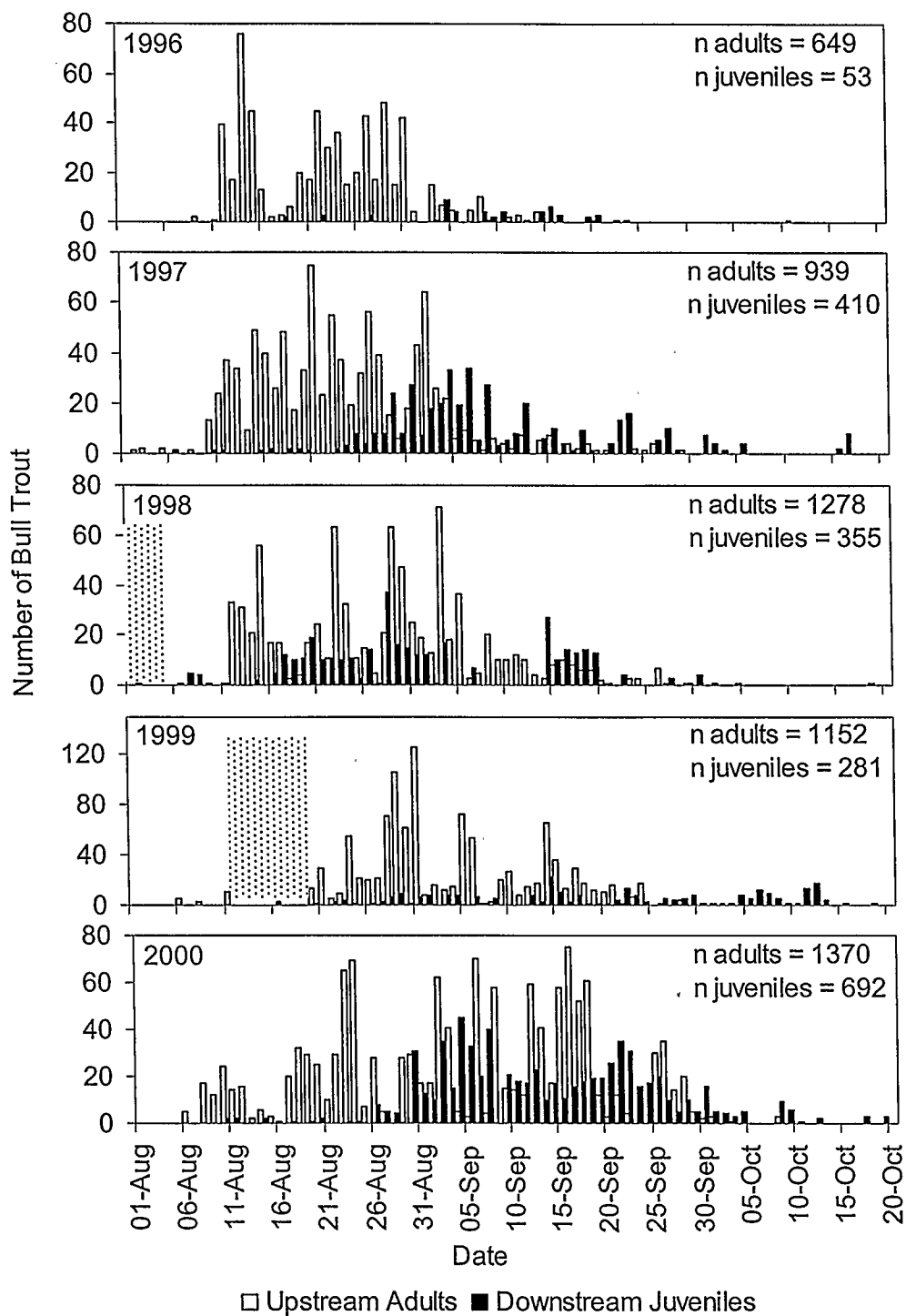


Figure 2.4 Timing of upstream migration of adult bull trout and downstream migration of juveniles in Smith-Dorrien Creek caught in the trap from 1 August until mid-October. In 1998, a 4 m opening in the fence was present from 31 July to 5 August (shaded area), during which at least 465 adults moved upstream. A similar breach in 1999 from 11 to 20 August is suspected to have allowed 90 adults to move upstream.

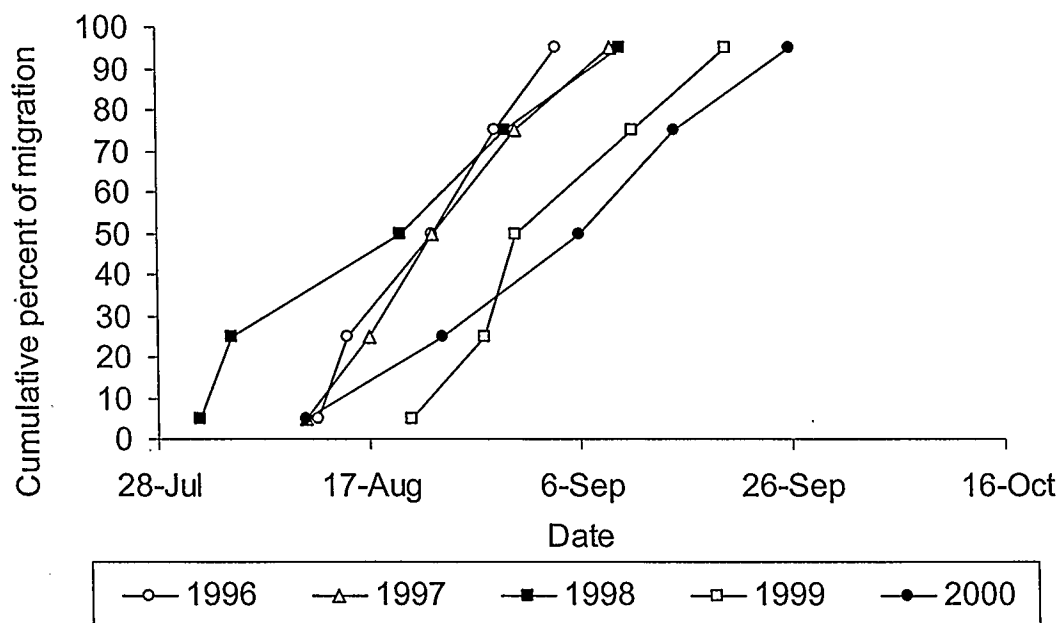


Figure 2.5 Cumulative percent of upstream migration of adult bull trout over time for each year. Points within each year represent cumulative migration levels of 5, 25, 50, 75 and 95% respectively.

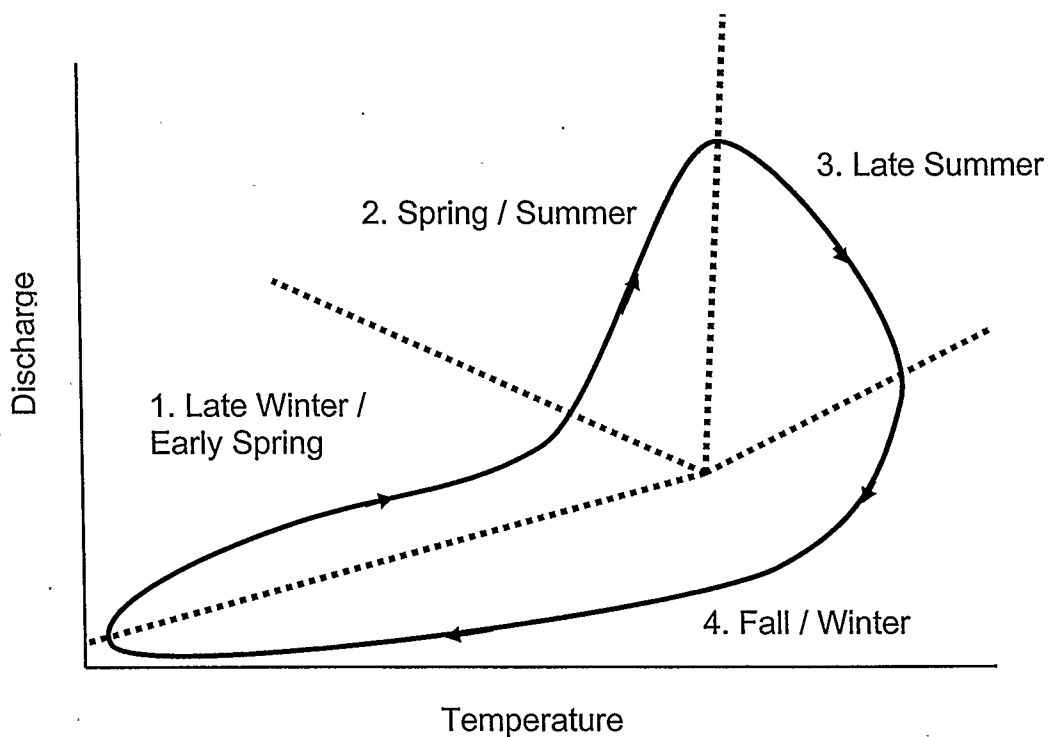


Figure 2.6 Schematic of the cyclical relationship between discharge and temperature each year. This figure can be broken into four key events throughout the season: 1. increasing temperature with low flows in late winter / early spring, 2. rapid increase in discharge in late spring / early summer with the onset of spring runoff. Temperature remains relatively constant due to the mediating effects of the snow pack, 3. decline in discharge in late summer as the snow pack declines, and extended daylight leads to maximum daily temperatures, 4. steady decline in discharge and daily temperatures as photoperiod is reduced into the winter where temperature and flow remain low and constant.

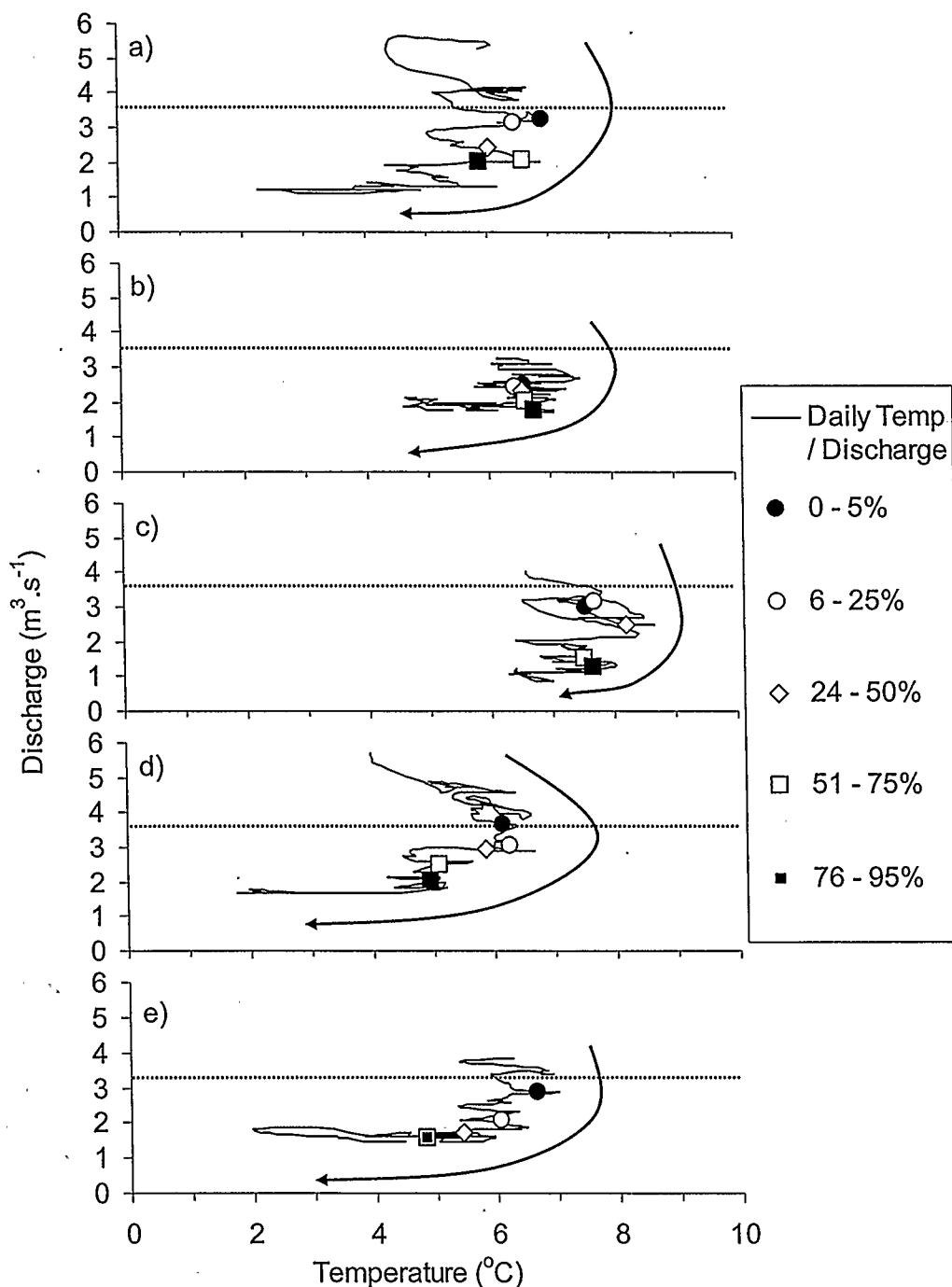


Figure 2.7 Seasonal discharge-temperature relationship in Smith-Dorrien Creek from 15 July to 30 Sept. each year (1996 (a) to 2000 (e)). Symbols represent the weighted mean migration temperature and discharge (Quinn et al. 1997) over the period when the associated proportion of adults moved into the creek, i.e. solid circle represents weighted mean temperature and discharge over the period that the first 5% of adults moved into the creek. Arrows indicate general direction of discharge-temperature relationship. Horizontal dashed lines indicate level where discharge equals  $3.5 \text{ m}^3 \cdot \text{s}^{-1}$ .

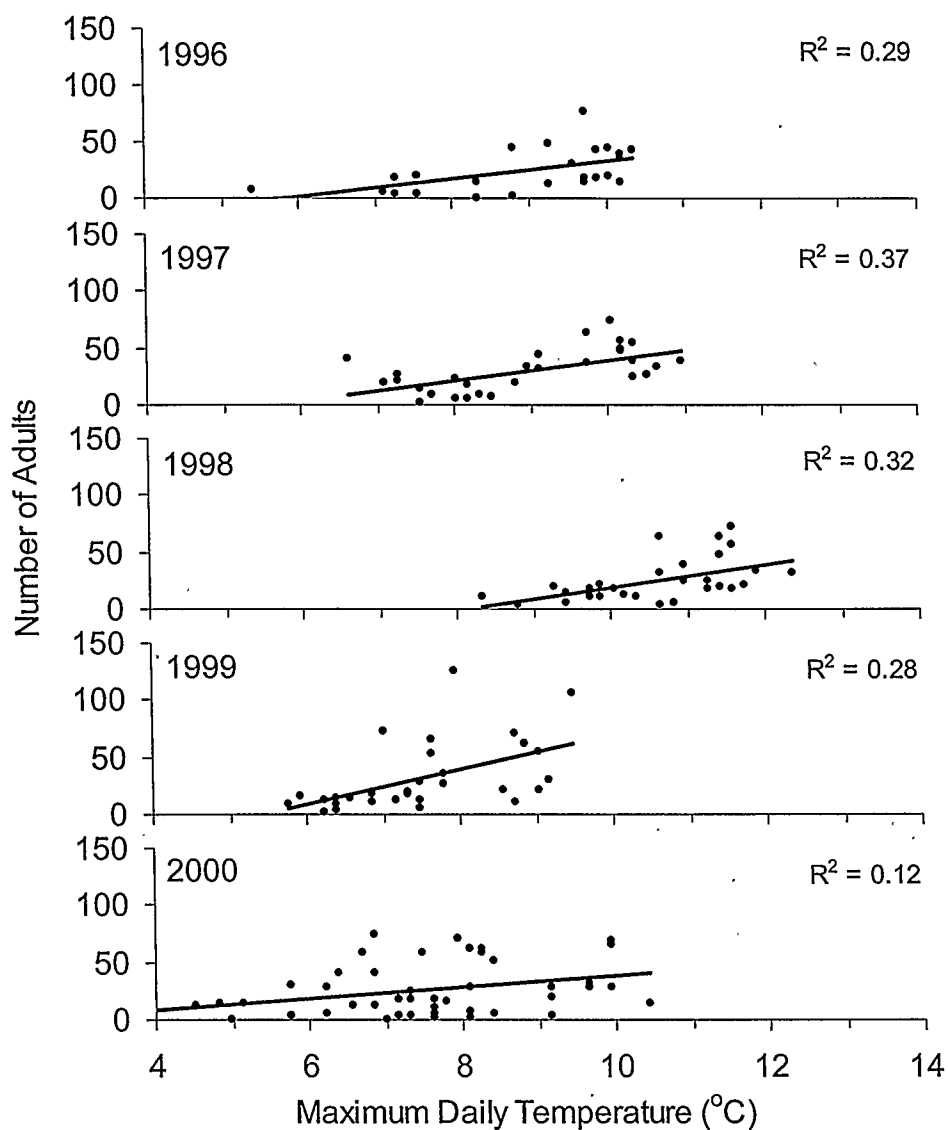


Figure 2.8 Number of adult bull trout migrating upstream each night in relation to maximum daily temperature. Linear regression best fit lines are displayed with corresponding R-squared values. In all years, a significant positive relationship was observed between temperature and the number of adults migrating upstream.

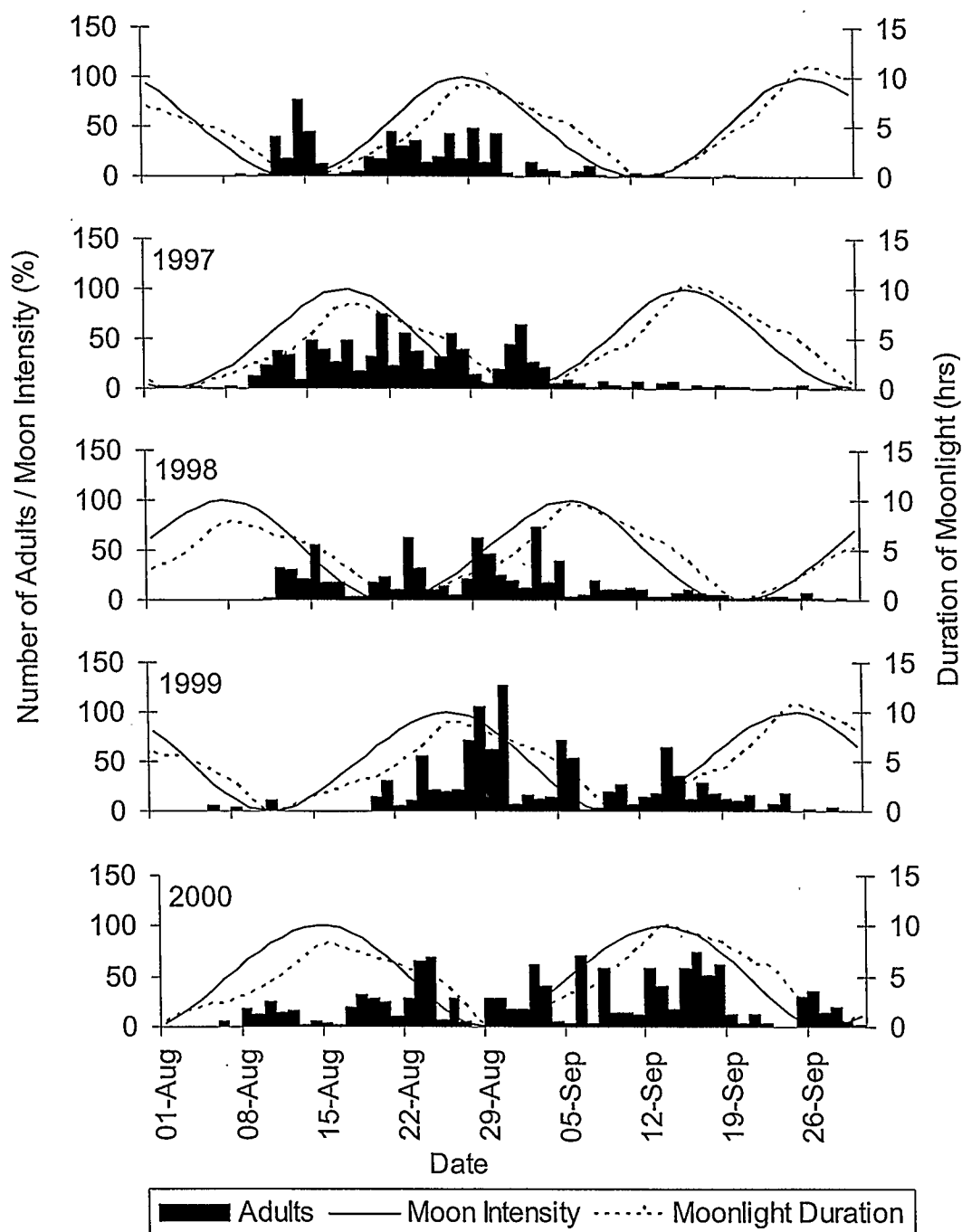


Figure 2.9 Number of adult bull trout migrating upstream each night in relation to moon intensity and moonlight duration. At 100%, moon intensity is synonymous with a full moon and at 0% with a new moon. Moonlight duration is measured as the amount of time that the moon is in the sky between evening and morning twilight. Shaded areas in 1998 and 1999 indicate periods when the trap was inoperable.

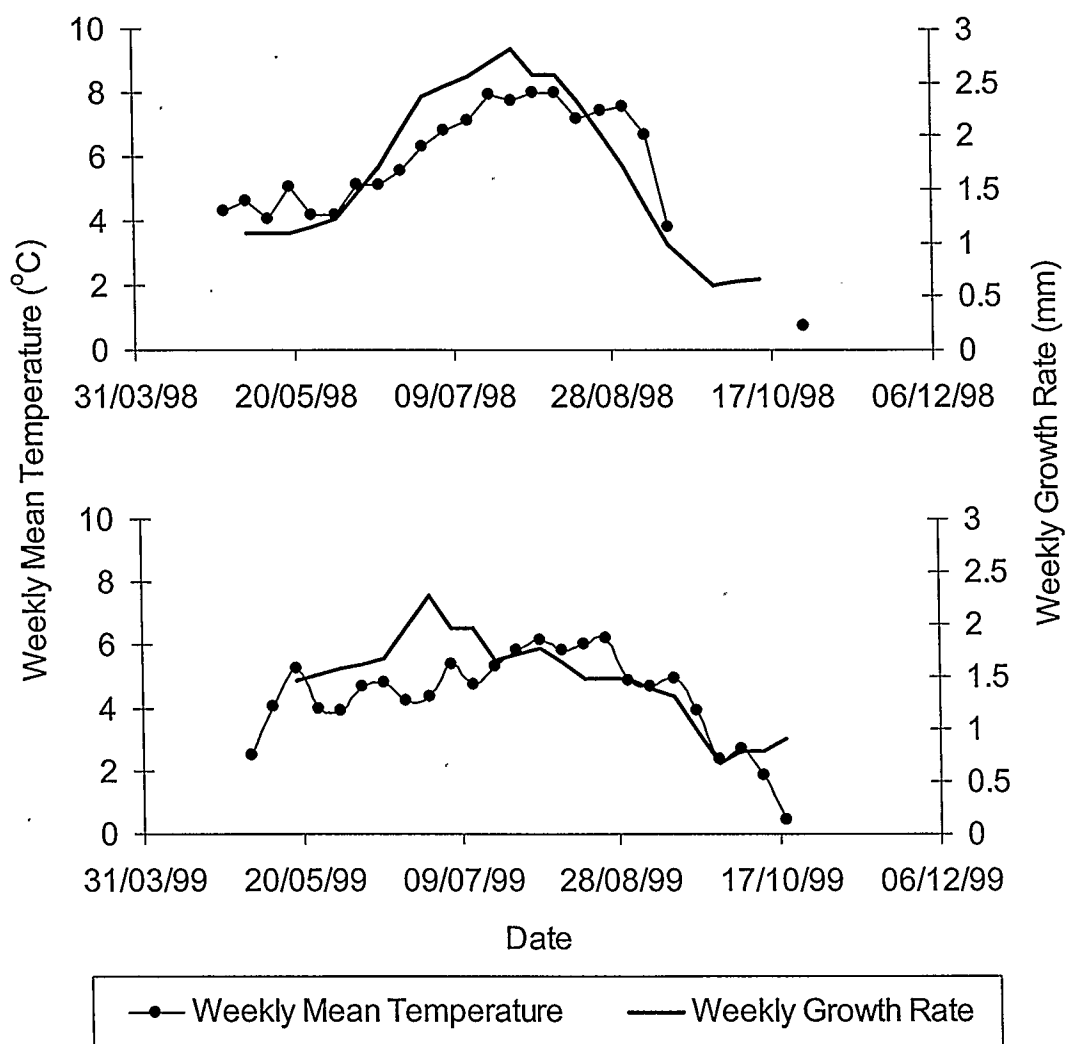


Figure 2.10 Weekly growth rates of juvenile bull trout and mean weekly temperatures in Smith-Dorrien Creek for 1998 and 1999.



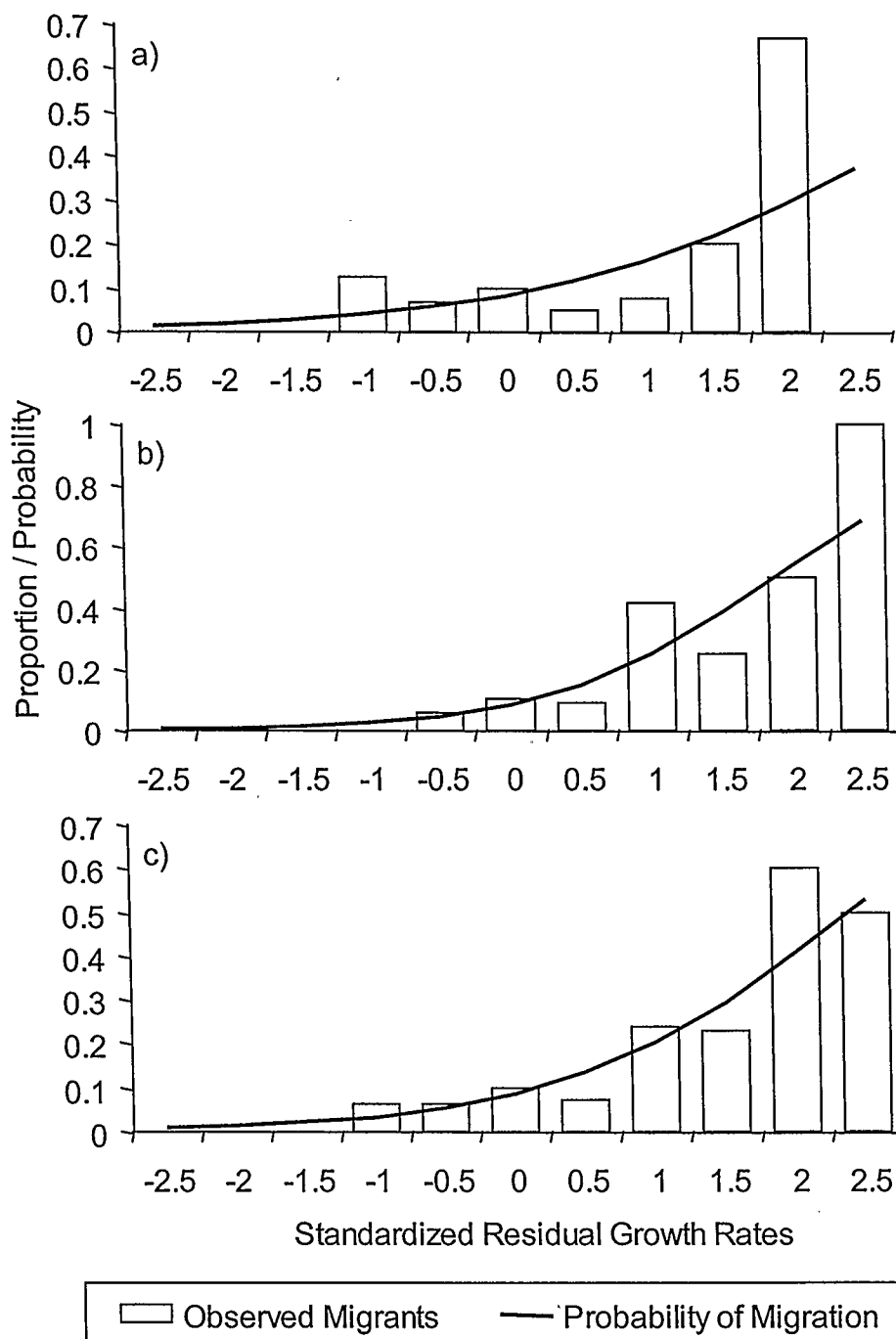


Figure 2.11 Proportion of juveniles migrating downstream in a) 1998 b) 1999 and c) both years combined, relative to the difference of the weekly growth rate from the mean. Due to unequal variance between months, growth rates were standardized by dividing by standard deviation. For individuals with multiple measurements, the standardized growth rate was averaged. Based on results from log likelihood analysis, the line predicts the probability of a fish within each growth rate category migrating downstream.

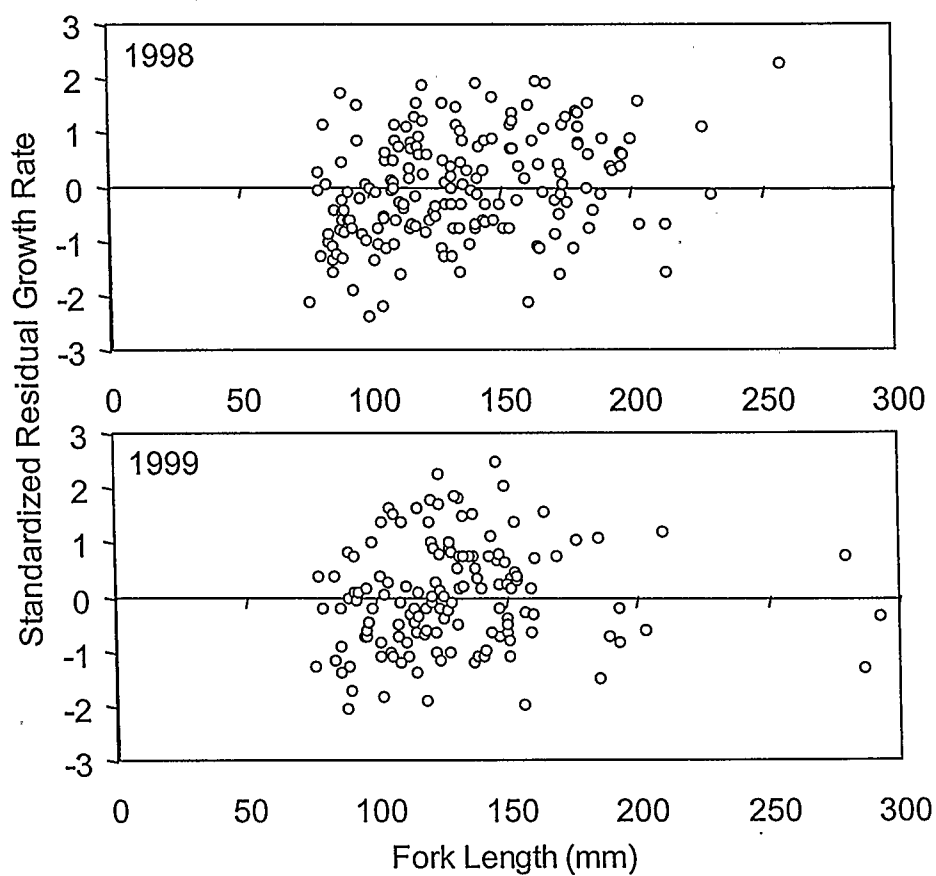


Figure 2.12 Standardized residual growth rates from the mean in 1998 and 1999 over the range of fork lengths sampled in Smith-Dorrien Creek. In 1998, growth rates were size dependent with larger fish having higher growth rates. Growth rates were not size dependent in 1999.

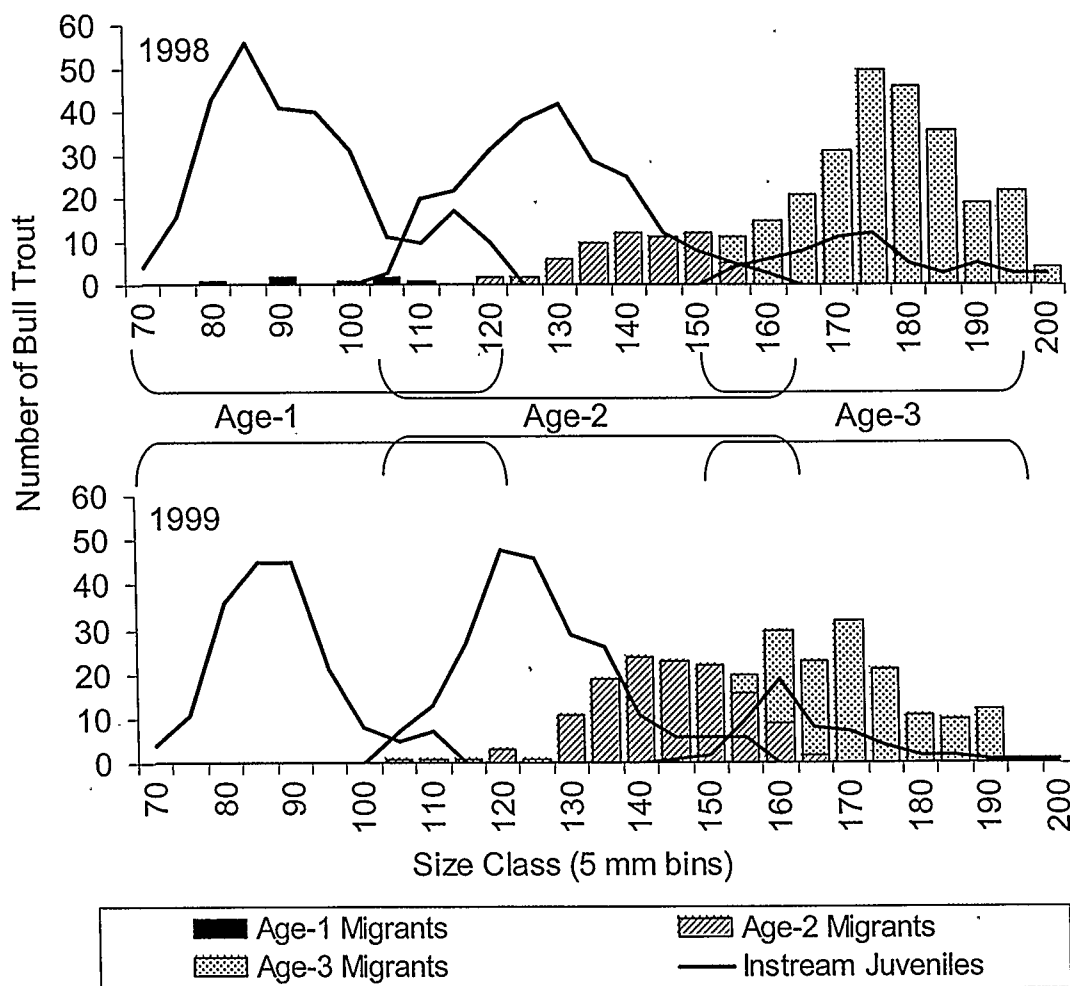


Figure 2.13 Length-frequencies of juvenile bull trout captured in Smith-Dorrien Creek (lines) and juveniles captured migrating downstream out of the creek (bars) in 1998 and 1999.

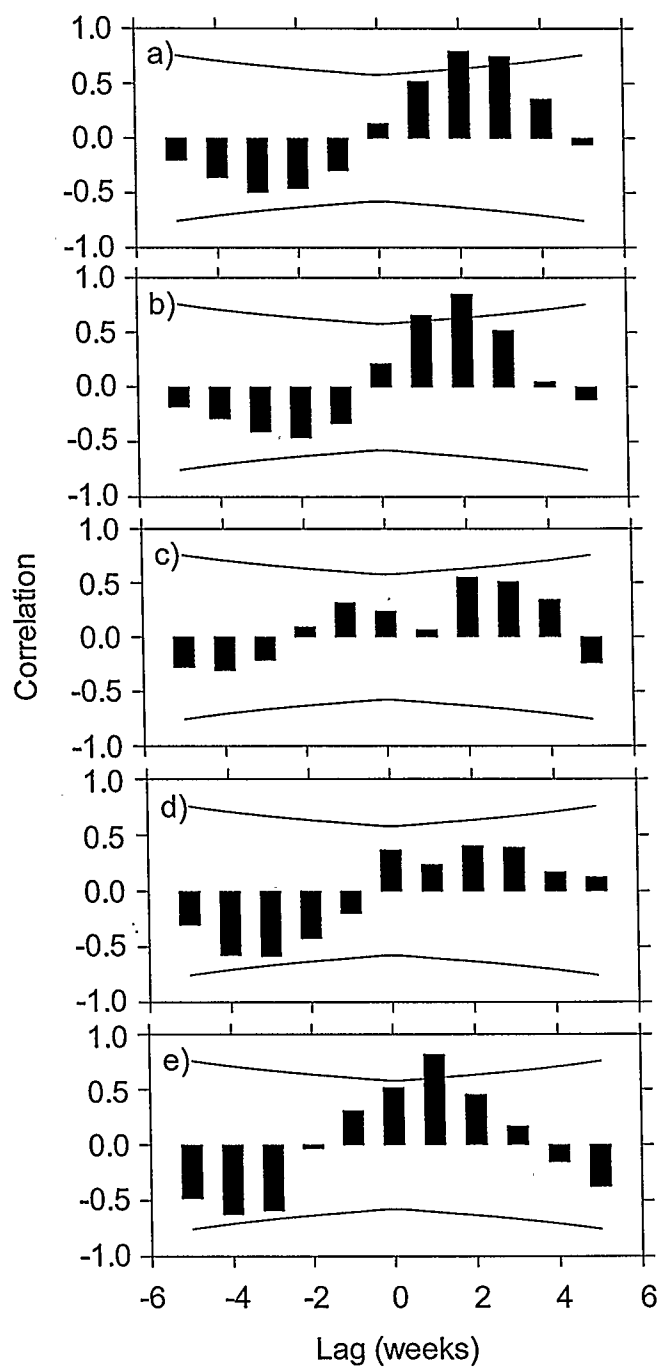


Figure 2.14 Cross-correlation plots between weekly upstream counts of adults and weekly downstream counts of juveniles for years 1996 (a) to 2000 (e). For example, in 1996 (a), the downstream migration of juveniles was positively correlated with the upstream movement of adults two weeks previous. The correlation value at lag zero is the Pearson correlation. The curved lines indicate 95% confidence levels for the significance of each correlation.

## Chapter 3 – Diel and seasonal movements of juvenile bull trout and refuge preferences

### 3.1 Introduction

For stream dwelling salmonids, predation risk is often managed through the use of cover, either in the form of physical refugia from predators or in the form of habitats in which predators are inefficient, such as turbid water or darkness (Bradford and Higgins 2001). At low stream temperatures, many juvenile salmonids (*Salmo* spp., *Oncorhynchus* spp.) switch from diurnal to nocturnal activity patterns, concealing themselves in interstitial refuges during the day, and emerging at dusk to feed (Campbell and Neuner 1985; Hillman et al. 1992; Riehle and Griffith 1993; Fraser et al. 1995; Bradford and Higgins 2001). These behaviour patterns could be viewed in the context of individuals making decisions about the trade-off between foraging and the risk of predation (Bradford and Higgins 2001). Although juvenile salmonids may also be more efficient foragers during the daytime (Fraser and Metcalfe 1997), they may be more vulnerable to visually based piscivores (Metcalfe et al. 1999). The period around dusk can be an important time for stream-dwelling salmonids as invertebrate drift often increases while the reduced light levels reduce the risk of predation (Rader 1997).

Activity of juvenile bull trout in streams varies on a diel basis. In most systems juveniles rest in refugia during the day (Thurrow 1997; Goetz 1997a; Bonneau and Scarnecchia 1998) and actively feed in the stream at night. Diet consists primarily of benthic organisms and instream drift (Nakano et al. 1992). Bull trout are found close to the substrate while feeding and rarely feed on terrestrial insects at the surface as

evidenced by the absence of terrestrial insects in juvenile stomach samples (Mushens et al. 2003). Daytime refuges vary depending on substrate and cover available and include; undercut banks, woody debris and rocky substrate (Shepard et al. 1984). Because many populations of juvenile bull trout are found in higher elevation, cold water streams, woody debris and undercut banks are often less available and the rocky substrate becomes the primary source of daytime refuge.

Many of the studies that have documented changes in habitat use between day and night have done so using visual snorkeling techniques. This technique is limited as it is based only on data collected from observations of unidentified fish. Data are also biased towards fish that are visible to the snorkler (Baxter and McPhail 1997; Goetz 1997a). Fish that may be hiding under rocks for refuge are less likely to be represented. Information on the movement and change in habitat use of individually marked bull trout has not been assessed.

Thurrow (1997) documented the habitat use of juvenile bull trout in a second-order central Idaho stream. Observations were conducted during both day and night by snorkeling. All fish observed during the daytime counts were concealed beneath “home stones” in pool and run habitats. A diel behaviour shift was observed with juvenile bull trout moving out of daytime concealment during the night to feed. Thurows’ description of a “home stone” for daytime refuge seems to suggest that individual bull trout may return to a preferred refuge each morning, although no fish were tagged and therefore individuals were not tracked over multiple diel periods. One of the limiting factors in the use of snorkeling observations is the inability to track individuals over time. Even if fish were tagged, the observer would be required to overturn numerous rocks to determine the

new daytime position of a tagged fish. Juvenile bull trout have been described as territorial (Goetz 1989), although little is known about the range over which an individual may be found over time. I hypothesize that juvenile bull trout would attempt to reduce the distance traveled on a daily basis between feeding habitat and daytime refuge in order to minimize energy expenditure and allow for an expedient escape if attacked. Therefore, the maintenance of a stable daytime refuge or “home stone” would be advantageous. A safe and reliable daytime refuge may provide a stable base from which juvenile bull trout would be able move out at night to feed and maintain a defined home range.

Gerking (1959) proposed a theory that adult stream fish are sedentary, often spending their entire lives within a single pool (Bachman 1984) or within a stream reach no longer than 20 m (Miller 1957). This restricted movement paradigm (RMP) (Gowan et al. 1994) has become the predominant view of fish behaviour within streams for the past 30 years and is supported by numerous studies, summarized by Gowan et al. (1994). Recent studies have provided increasing evidence to the contrary, finding movement to be relatively common in populations of stream-resident salmonids (Riley et al. 1992; Young 1994; Gowan et al. 1994; Gowan and Fausch 1996; Kahler et al. 2001). As Gowan et al. (1994) point out, data collection methods used in past studies are biased in favour of confined home ranges, as focus is placed on recaptures within a defined stream section and not on the actual movement of the fish. Methods employing the use of radio telemetry tags which allow repeated measures on individuals are now much more common.

Some detailed habitat use information has been collected on bull trout in streams using radio-telemetry tags, although in many cases tag size has limited the study to

migratory adults and resident adults over 230 mm in length (Jakober et al. 1998; Swanberg 1997). In many cases, this corresponds to age-4 and older bull trout. Because larger tags are used with batteries lasting 90 days and longer, sampling effort is spread out over the life of the tag and is usually addressing migrational movements of adult spawners. Therefore, virtually no diel habitat-use information has been collected using radio tags. Smaller radio tags are now available that permit study of the movement and habitat use of juvenile bull trout.

In summary, there is limited information on the diel habitat use and movement of individual juvenile bull trout over time. Such information would be beneficial in determining the habitat and range requirement of individual bull trout. Many tributary streams have been adversely affected by various land-use practices, and stream rehabilitation programs require information on habitat requirements of juveniles (Berry 1997).

This chapter addresses three questions:

- (1) How far do juvenile bull trout move on a daily basis between daytime refuge and nighttime feeding location?
- (2) Do juvenile bull trout show fidelity to specific daytime refuges or “home stones”?
- (3) Does juvenile bull trout habitat use at the time scale of hours to seasons support the restricted movement paradigm?



## **3.2 Methods**

### **3.2.1 Study Area**

All field work was conducted in Smith-Dorrien Creek (50° 44' 31" N, 115° 14' 36" W), a tributary to Lower Kananaskis Lake in Kananaskis Country, Alberta, on the Eastern slopes of the Rocky Mountains approximately 150 km west of Calgary. The stream is 13 km in length and flows year round. Primary sources of water include snow melt from the surrounding ranges and groundwater upwelling. Two study areas were set up in Smith-Dorrien Creek. The first section (Section 2) was 1580 m in length and was located 4.3 km upstream from Lower Kananaskis Lake (Figure 3.1). Section 3 was 4.7 km upstream of Section 2. It included 1260 m of the main stream and 265 m of James Walker Creek (JWC), a small tributary that enters Smith-Dorrien Creek 320 m upstream of the lower boundary of Section 3.

### **3.2.2 Long-term habitat use and movement**

To determine long-term habitat use and movement, sampling occurred approximately every three weeks from May through October in 1998 and 1999. Sections 2 and 3 were each sampled 10 and 9 times in 1998 and 1999, respectively. All sampling occurred from one hour after sunset until the section was completed or dawn, whichever came first. If a section was not completed in one night, it was finished the following night from the point where the previous night's sampling left off.

Fish were captured by night netting, a technique adapted from Bonneau et al. (1996). This consisted of walking upstream with halogen dive lights until an individual

fish was spotlighted. Once a fish was located, a dip net (0.6 mm dark-green mesh with an opening of 0.2 X 0.6 m) was placed 0.2 m downstream of the fish. The fish was then coaxed into the dip net from upstream using a rigid nylon sieve attached to a pole. Each bull trout was mildly anaesthetized (tricaine methane sulfonate – MS 222), after which the fish was measured (nearest 1 mm) and then marked using Passive Integrated Transponder (PIT) tags (Prentice et al. 1990). Each tag, measuring 12 mm long by 2 mm in diameter, was inserted into the body cavity using a 14-gauge hypodermic needle modified with a stainless steel ramrod attached to the plunger. Tags were inserted approximately  $\frac{3}{4}$  of the way between the pectoral and pelvic fins and just to the side of the ventral line. The needle pierced the skin after which the tag was inserted by depressing the plunger. The minimum size tagged was 75 mm FL, corresponding to age-1 fish.

The location of each fish was measured using a GPS receiver at the time of capture. These coordinates were later differentially corrected using the base station located at Barrier Lake Field Station. This permitted the accurate positioning of juvenile bull trout to within one metre of its actual location. Habitat characteristics recorded for each fish included, stream depth, habitat unit type (riffle, run, pool), and substrate based on a simplified Wentworth scale (Nielson and Johnson 1993) as fines (< 2 mm), gravel (2 - 64 mm), cobble-boulder (> 64 mm) and bedrock. Distance traveled from a previous position was calculated at later date by analyzing the GPS coordinates using a GIS vector-based program (Cartalinx, Clark Labs, Clark University). Distances were not calculated as the crow flies, but instead as the fish swims. Distances moved by fish were

determined by measuring the distance between the two points following the layout of Smith-Dorrien Creek.

### **3.2.3 Short-term habitat use and movement**

Radio tags were used to determine short-term habitat use and movement of juvenile bull trout. Juvenile bull trout between 150 – 200 mm in length were captured by night netting within study sections 2 and 3 in August and September 1998, and July, August and September 1999 (Table 3.1). Micro-radiotags (Lotek Engineering Limited, 0.75 g in air, 0.5 g in water, 12 mm x 5 mm x 7 mm) with unique frequencies were surgically implanted into 39 bull trout (Table 3.1). Data from 35 fish were used as batteries in two tags died within 5 days of deployment, and lack of movement and location of two other tags suggested that these fish may have died or the tags were shed.

Bull trout were anaesthetized in 10 L of river water with 1.5 ml·L<sup>-1</sup> clove oil/ethanol mixture (0.5 ml clove oil emulsified in 4.5 ml ETOH). After anaesthesia was induced (i.e., after regular opercular movement had ceased), fork length (mm) and weight (g) were recorded and a Passive Integrated Transponder (PIT) tag was applied to ensure identification after the radio tag had expired. Fish were then placed dorsal side down into foam padding in which slits had been cut to provide support during surgery. Head and gills were submerged in 8 L of aerated river water with a maintenance concentration of 1 mm·L<sup>-1</sup> clove oil/ETOH anaesthetic. A 1-cm incision was made posterior to the left pelvic fin. A small puncture was made, using an 18 G hypodermic needle, anterior and slightly lateral to the vent, through the body wall. A 150 mm spinal-tap needle with a

blunt tip was then inserted into the puncture, through the body cavity, and out the incision. The 30 cm antenna of the transmitter was then inserted into the tip of the needle which was subsequently withdrawn, leaving the antenna threaded through the puncture near the vent. The transmitter was inserted into the body cavity and the incision was closed with one or two sutures of Ethicon 1-0 non-absorbable braided silk. Surgery and recovery required < 10 min. There were no obvious behavioural differences among fish before or after they were tagged, and clove oil anaesthetic has been shown to have negligible post-surgical effects on the behaviour of small salmonids (Anderson et al. 1997). After the procedure, fish were released at the site of capture after one hour of observation to ensure full recovery.

Fish movements were monitored using a sequential scanning receiver (Lotek Eng. Ltd. SRX\_400) and a hand-held directional antenna. Tracking was conducted by foot. The location of each fish was determined twice daily; once during the day and again at night at least one hour after darkness. All fish locations were pinpointed to < 1 m. Tagged bull trout locations were usually confirmed visually. During the daytime while in refuge, accurate fish location was determined using the telemetry receiver but on occasion was confirmed by searching for the tag antenna extending from the refuge. At each fish location, a stake with numbered flagging was inserted for future identification. All fish locations were entered into a Trimble backpack GPS unit and later differentially corrected to <1 m accuracy.

At each location, the stream unit used by the fish was identified as pool, riffle or run. Water velocity was measured at three points; immediately below the surface, at 0.6 of maximum depth (average velocity) and at the substrate, with a Marsh-McBirney Flo-

Mate Model 2000 velocity meter. Substrate was recorded based on a simplified Wentworth scale (Nielson and Johnson 1993). The type of cover used was divided into four categories that included undercut banks, overhanging vegetation, woody debris and boulders. Undercut banks were classified as cover if the distance between the water surface and the underside of the bank was less than 25 cm. Overhanging vegetation was defined as living plants within 25 cm of the river surface. Distance measurements collected included stream depth, distance from previous position (including direction (i.e. upstream or downstream)), distance to nearest cover and distance to nearest adult, if present. To reduce the effect of samplers on fish behaviour, all habitat and fish movement measurements for day and night time locations were collected during the day when fish were in refuge habitat. All fish locations were determined with telemetry both before and after habitat measurements were taken to ensure that samplers did not influence fish movement. Distance measurements calculated using Cartalinx included nighttime range, daytime range, overall range and displacement. Nighttime range is the measurement between the most upstream and downstream position a fish was found at during nighttime observations. Daytime range measures the distance between the most upstream daytime refuge and the most downstream location. Overall range is the measurement between the most upstream and downstream location regardless of time of day. Displacement is the distance measured between the location where a fish was first observed and the location where the fish was last observed before the tag expired.

### **3.2.4 Analysis**

Data from all recaptured fish were used in analysis of fish movement. For analysis associated with the restricted movement paradigm, fish captured for the first time during each sampling event in 1998, were assigned to a sampling cohort (Table 3.2). Fish from these cohorts were tracked over nine additional sampling events to determine capture efficiency and what proportion of fish remained within a study section. Because the time period between sampling events varied and may have an effect on the number of fish lost from a cohort, a weekly loss rate was calculated that removed the bias of time.

Data for habitat use by radio-tagged fish were grouped by day or night and pooled together. Only one habitat measurement for each day or night location was used (no repeated sampling of the same location). Habitat characteristics including substrate composition, cover present and stream velocities were compared between day and night within each category (i.e. runs, riffles, pools) using Chi-square analysis. Habitat use (number of day and night locations in each habitat unit) was compared to the number of metres of habitat available within the two study sections. Data for habitat availability collected in 1996 during a stream-wide habitat survey were used (Mushens, unpublished data).

## **3.3 Results**

### **3.3.1 Home range / Restricted Movement**

A total of 953 individual fish were captured in 1998 and assigned to each of the ten sampling cohorts. These ten cohorts were tracked over ten additional sampling

sessions from May 1998 to October 1999. Mean capture efficiency over all cohorts was 38%. The recapture rate for each sampling cohort was tracked through time. An average of 37% of fish was recaptured during the first recapture event of each sampling cohort (Figure 3.2a). In contrast, an average of 79% of the remaining fish in a sampling cohort was caught in successive sampling events. This may indicate the presence of two behaviour types. The initial 63% that were never recaptured within the sites where they were initially marked were mobile fish, while the remaining 37% could be classified as sedentary/stationary fish. Seasonal variation in the loss rate was not evident (Figure 3.2b). The Weekly loss rate for fish after being tagged initially was consistently higher than that of fish caught in subsequent sampling sessions. Weekly loss rates for the October sample indicate that losses are extremely low over winter and fish move very little (Figure 3.2b).

Between 5 May to 24 October 1998, and 8 May to 26 October 1999, a total of 1462 fish were captured using the night netting technique and received a PIT tag. The mean number of fish caught during each sampling session was 117 (range 65 - 204). The mean overall displacement of recaptured fish was 79.5 m with a median of 12.1 m ( $n = 476$ ), suggesting that most fish remained close to “home” with a small number found up to 4800 m away (moved from section 3 to section 2). Of the 476 PIT-tagged fish that were recaptured in the creek, 335 (70.4 %) had moved less than 100 m from the point of initial capture and 175 (36.8 %) were found within 10 m of the point of capture. Most fish were captured close to the point of initial capture and distance from the point of initial capture approximately followed a decreasing power function (Figure 3.3). Fish that were recaptured were not necessarily captured in every successive sampling event.

Capture efficiency using the night-netting technique for all 1476 fish was 33%. With each successive sampling event, the probability of capturing a particular fish increased in relation to one minus the proportion of fish missed ( $1 - \text{capture efficiency}$ ) raised to the power of the number of sampling events. For example, with three successive sampling events, the probability of capturing a particular fish if it remains within the study section would be  $1 - (0.67)^3$  or 0.70, and after nine sampling events would be 0.97. Therefore it is unlikely that many of the fish that were not recaptured remained within the study section. These fish likely moved outside the boundaries of the study section, indicating high movement distances, or died.

A total of 80 (16.8 %) recaptured fish were captured at the mouth of Smith Dorrien Creek, moving into Lower Kananaskis Lake (Figure 3.4). Excluding fish that migrated into the lake (Chapter 2), size of fish did not have a significant effect on the distance moved (ANCOVA:  $F = 1.47$ ,  $df = 340$ ,  $P = 0.23$ ). When movement was divided into three time periods: before adult presence (May-August), during adult presence (August- early October) and post adult presence (late October), there was no significant relationship between distance moved and size in each of the time periods (ANCOVA:  $F = 0.84$ ,  $df = 338$ ,  $P = 0.36$ ).

For many fish, overall displacement was much smaller than the overall range of movement. A number of fish exhibited movement away from the point of initial capture throughout the season but returned close to the initial capture point (Figure 3.5). As indicated in Figure 3.5, points that are located on the 1:1 line represent fish whose overall displacement equaled the range of movement. Points that are located below the line indicate fish whose overall displacement was less than the range over which the fish had



moved. Fish that moved over 200 m in distance were more likely to be moving unidirectionally. Fish for which the overall range of movement was less than 200 m were more likely to move in both directions throughout the range, therefore reducing the overall displacement in comparison to the range. Results from PIT tagged fish indicate that some fish moved up to 200 m in one direction and then returned back as much as 120 m. The frequency of sampling with night-netting is low enough and the time between sampling large enough that fish movement may be more complex than is indicated. Results from movement data from 35 radio-tagged fish tracked daily over a period up to three weeks (Figure 3.5) have much higher resolution. Fish moved as much as 200 m away from the point of initial capture, yet returned to within metres of their original location. Similar to results from night netting, fish that moved beyond 200 m generally moved unidirectionally to a new location. In both cases, for fish that showed complex movement, displacement was commonly less than 50 m, but the overall range could extend as much as 200 m.

### **3.3.2 Distance Moved Between Day and Night**

The distance that juvenile bull trout traveled from their previous daytime position to a nighttime feeding area was significantly greater than the distance between the past and present daytime position (ANOVA:  $F = 5.04$ ,  $df = 854$ ,  $P = 0.03$ ). This indicates that if a fish moved to a new area, it moved back the way it came to find a daytime refuge instead of moving into an area where it had not been before. As such, the overall nighttime range of an individual juvenile bull trout (distance from most upstream to

downstream point during night forays) was greater than its daytime range (Paired t-test:  $t = -3.45$   $df = 31$   $P$  (one-tailed) = 0.001; Figure 3.6). Sixteen of the 32 fish tested maintained smaller daytime ranges in comparison to their nighttime range. The remaining 16 extended their daytime range with their nighttime range, finding refuge close to the extent of their nighttime forays.

Juvenile bull trout appeared to show fidelity to daytime refuge locations. The number of daytime refuges maintained by a juvenile was significantly lower than the number of nighttime foraging locations (Paired t-test:  $t = -5.35$ ,  $df = 31$ ,  $P$  (one-tailed) < 0.0001). Although the length of time that each tag was active varied (mean 17 days, range 8 – 22), it did not have any significant effect on the number of daytime locations recorded for each fish (ANOVA:  $F = 0.04$ ,  $df = 35$ ,  $P = 0.85$ ). There was much variation in the number of nighttime locations in comparison to daytime locations (Figure 3.7). For example, eight fish maintained only 1 daytime refuge, while the number of nighttime locations ranged from 1 -14. A total of 22 fish maintained 4 or fewer daytime refuges.

When the combination of day and night locations, diel movement and overall displacement is addressed, fish can be divided into different categories that relate movement, displacement and fidelity (Table 3.3). If fish can have either high or low movement, displacement and refuge fidelity, a total of six combinations are possible. Fish with low movement and displacement are generally found in a small area less than 50 m in length, but can exhibit high or low refuge fidelity. Fish may also exhibit high movement (>50 m) and low displacement with either combination of refuge fidelity. Combinations with low movement and high displacement are not possible as

displacement cannot exceed movement. Fish that show high movement and displacement can show refuge fidelity for a time and then move large distances usually associated with migration out of the natal stream. Other fish that are highly mobile tend to show low fidelity to a particular home stone. Examples of these behaviours are presented in Figure 3.8. Fish 148.980 displayed high fidelity to a daytime refuge with a low displacement but very high range of movement to nighttime feeding areas. Fish 149.310 showed similar trends but with low range of movement. Fish 149.380 showed no fidelity to one location with high numbers of day and night locations, but had a very low range of movement and displacement. Fish 149.240 was recorded to have moved only one night in 17. The final two fish (149.340 and 148.990), exhibited a high range of movement as they moved towards Lower Kananaskis Lake, but 149.340, had a very small home range before migrating downstream, while 148.990 displayed erratic movement and no fidelity to a daytime refuge.

Some fish exhibited very little movement throughout the life of the radio-tag. To determine whether fish move out at dusk every night, fish 149.260 was monitored over five time intervals in one night starting before dusk (Figure 3.9). This fish, which was normally active immediately after dusk, was still in refuge when normally inspected and was still in refuge two hours later. When inspected four hours after dusk, the fish had moved 2 m from refuge, and was found an additional 16 m downstream four hours later, before returning to the same daytime refuge. Although one sampling event provides only anecdotal information, it raises the question whether fish that did not move out of refuge by the time sampling occurred may have moved out to feed at a later time.

### 3.3.3 Predator Avoidance

The initiation of downstream movement of juvenile bull trout on several occasions suggested predator avoidance behaviour. In addition, two juveniles were confirmed to have been eaten by adults. One was by radio telemetry signal that moved only with a spawning adult and the second by the identification of a PIT tag from a juvenile located inside a resident adult. During July 1999, while moving over 7 km downstream, fish 148.990 took refuge in a feeder stream to Smith-Dorrien Creek measuring less than 0.3 m in width and only 0.2 m in depth. The fish resided there for six days before continuing its migration downstream. In August 1998 and 1999, two different fish (149.340 and 149.020, respectively) migrated over 3 km downstream out of Section 3 and accessed the same small outlet stream from a beaver pond. The stream was only 0.25 m wide and 0.2 m deep. Fish 149.340 remained in the stream for two days before continuing downstream (see Figure 3.8, Aug. 16-18). The second fish (149.020) moved up the outlet stream into the beaver pond and remained there for the extent of the life of the radio-tag. Fish 149.020 had previously exhibited fidelity to one location in Section 3 before moving downstream. Upon inspection of the previous site the day after the migration, several adult bull trout were observed in the vicinity. This behaviour is not altogether uncommon or unexpected. While conducting night netting in both 1998 and 1999, field crews noticed on numerous occasions that some pools contained large numbers of juvenile bull trout and no resident adults. On later sampling sessions, these same pools were observed to contain one or two resident adults and no juveniles. It is likely that the juvenile bull trout vacated the pool to reduce the risk of predation.

### 3.3.4 Habitat Preference

Pools and runs were the most common habitat unit used by bull trout during both day and night (Figure 3.10). Although riffles are widely available, use by juvenile bull trout was extremely low. Habitat use in pools and runs during both day and night was much higher and riffle use much lower than expected based on availability and chance alone (day chi-square = 162.3 df = 2  $P < 0.0001$ ; night  $\chi^2 = 297.1$  df = 2  $P < 0.0001$ ). Habitat use by cover and substrate composition differed significantly between day and night use (Table 3.4). Substrate composition of pools used at night was primarily fines followed by cobble/boulder, whereas pools used during the daytime were predominately cobble/boulder followed by fines and gravel (Figure 3.10). Undercut banks and woody debris availability were high in both day and night pool locations, whereas availability of cobble/boulder used for refuge was almost twice as high in daytime pools as compared to nighttime pools. There was no significant difference in stream velocities between respective habitat units and day and night use (Table 3.3).

## 3.4 Discussion

Bull trout habitat use and movement was assessed at various temporal and spatial scales. Time scales included diel, involving movement and habitat use between day and night in the scale of hours, daily for a period of up to three weeks, and seasonally at approximately three week intervals over a period of six months. Spatial scales included detailed movements in the range of metres, to reach-scale involving two 1500 m sections, to drainage scale involving the downstream migration of juvenile bull trout into Lower

Kananaskis Lake. Although there is variation in overall movement and home range of juvenile bull trout, they can be categorized as either sedentary or mobile. Mobile individuals appear to account for a larger proportion of the population. Apart from fish that migrate downstream to Lower Kananaskis Lake, size does not appear to influence movement distances of juvenile bull trout.

Based on results, a proportion (at least 33%) of juvenile bull trout maintain home ranges and show fidelity to particular daytime refuges that support the restricted movement theory. The 67% of fish that were never recaptured suggest a highly mobile contingent, although sampling methods, capture efficiency, and individual fish behaviour likely affect this result and likely provide an overestimate of mobility. As indicated by telemetry results, apart from bull trout that moved downstream into Lower Kananaskis Lake, most fish maintained defined home ranges that included a small daytime range and larger nighttime range. Although radio tags were restricted to fish 150 mm and greater in size, results from night-netting data show that fish size did not influence distance moved by fish. Juvenile bull trout showed fidelity towards particular daytime refuges, indicating that such habitat may be an important habitat requirement for fish with diel activity behaviour, and could be a limiting factor in some systems. Pools and runs with cobble and boulder substrate were favoured by bull trout for daytime use, whereas cobble and boulder substrate was not as common in nighttime feeding areas.

Based on recapture rates of bull trout juveniles from night-netting sessions, it appears that fish can be categorized as either mobile or sedentary. While I use the classification of mobile and sedentary fish, the categorization may be dependent on the temporal scale of the study. So what happened to the 63% (or 986 fish) that were never captured again

within the two study sections? As Gowan et al. (1994) point out, many studies overlook the high proportion of fish that are never recaptured and focus on the smaller proportion that are recaptured and the limited movement that they exhibit. If this smaller proportion does in fact represent fish that are “sedentary” and have found suitable refuge and feeding habitat, then it is not surprising to find that the home range of these fish is quite small. Mobile fish are an important part of any population as they provide a source from which disturbed (or enhanced) habitats can be recolonized (Heggenes et al. 1991; Hilderbrand and Kershner 2000). When considering the trade-off between extensive movement to find more profitable habitat, and resulting increased predation risk, it is expected though that once a mobile fish finds suitable habitat, it may adopt the sedentary behaviour. It is interesting to note that the weekly loss rate of fish from a sampling cohort was very low over the 6 month period from late-October 1998 to early-May 1999. By late-October, fish were likely settling into winter habitat and would not move much until increased water temperatures the next spring.

Measurement of the proportion of sedentary fish is a conservative estimate as there are many factors which may affect the ability to determine whether a fish is stationary. Bias associated with edge effects is common in studies where discrete study sections are set (Rodriguez 2002). Fish that are marked near the upper or lower boundary of the study section have a higher probability of being associated with movers, even though these fish have only moved a short distance outside the study section. The large size of each of the two study sections used here (1.5 km each) helps to reduce the influence that an edge effect may have on this measurement as compared to other studies, but the trade-off is capture efficiency within such large sections. Capture efficiency using the night-netting

technique was only 33%, meaning that fish that were classified as mobile may have remained within the study section for an extended period before moving (if at all) but were not captured.

Unless mobile fish move extensive distances in a short period of time (21 days) it is unlikely that a large number of fish were unaccounted for in this manner, as the recapture rate of tagged fish after the first recapture was high enough (79%) to assume that most tagged fish that were still in the study section were recaptured, and the probability of capturing an individual increases over successive sampling events. Data from radio tagged fish indicate that fish could move as much as 2.5 km within a night, although these individuals were undertaking a substantial, life-history related migration downstream to their adult habitat. This is not the case with PIT tagged juveniles as they would have been captured at the weir trap at the entrance to the lake (see Chapter 2). Low recapture after only the first capture event could also suggest that mortality associated with PIT tag application may be responsible. This is unlikely as one person with extensive experience was used to apply tags. Mortality associated with PIT tag application was assessed in the lab on juvenile rainbow trout (*Oncorhynchus mykiss*). Tagged fish were observed for one week and none of over 100 fish died as a result of PIT tag application (Paul, A.P., *pers. comm.*). Limited movement associated with the application of the tags is also unlikely as juvenile bull trout that received radio tags during a lengthy and more stressful procedure showed daily movements within a day of surgery. It is also unlikely that natural mortality rates in the range of > 50% would occur within the period of 21 days. Based on the distribution of recaptured juvenile fish in Figure 3.3, the number of fish extending beyond 100 m is very low and could not account



for the migration of 986 fish. I say this with caution as this distribution may be biased towards sedentary fish. The combination of high movement with low capture efficiency may allow fish to move beyond the confines of the study sections.

Nighttime movement behaviour as indicated by telemetry results (Figure 3.9) may also affect the ability to capture fish. Some fish may still be in the section but were not sampled because they were not visible to the sampler (i.e. did not come out of the refuge that night or until some time after the sampler had passed). If individual fish become active at different times throughout the night, then this could affect considerably what fish are captured in a particular section of stream. With a 1.5 km study section and sampling starting at the downstream end just after dusk and progressing upstream until just before dawn, each section of stream (i.e. lower 250 m as compared to 750 m upstream), is sampled relatively consistently at a different period of the night. If individual fish have different time periods of activity, then sampling at the lower end of the study section would only sample fish that become active early in the night, and sampling 750 m upstream would only capture fish that are active in the middle of the night. In other words, the strict time to space sampling regime may sample only a small portion of the fish that are physically present within that section of stream. As such, a fish may only have to move a small distance (250 m) from its initial location to become either visible or invisible to the sampler. In essence, the edge effect may still affect the ability to determine the migration rate of fish but the edge or boundary is temporal instead of physical.

A common guideline that has been used to identify restricted movement is 20-50 m (Gerking 1959; Gowan et al. 1994; Rodriguez 2002). My results indicate that although

overall displacement of over 50% of juvenile bull trout sampled by telemetry or recaptured by night-netting was less than 50 m, the range over which fish were active can extend well beyond this and is attributed to nighttime foraging sessions. Juvenile bull trout may move as much as 200 m away from the point of initial capture and return to, or close to, this point. There are studies that assess the home range of fish by determining positions over time while sampling during the daytime (i.e. Smithson and Johnston 1999). This would provide only an indication of the range of daytime refuges in the case of species that are nocturnally active. Nocturnal feeding behaviour is common in salmonids in streams when water temperatures fall below 8°C (Baxter and McPhail 1997; Goetz 1997b; Young 1998; Bradford and Higgins 2001). Bunnell et al. (1998) tracked brown trout (*Salmo trutta*) movement hourly for select 24 hour periods throughout the year. Results showed that fish exhibited nocturnal behaviour and the majority of fish moved up to 80 m during the night, but had a displacement of only 10 m from the initial point of capture. Hildebrand and Kershner (2000) observed that the home range of cutthroat trout increased depending on the time scale and timing when locating radio-tagged fish. Fish that were assessed weekly indicated a home range close to zero, whereas the addition of hourly sampling over a 24 hour period increased the home range up to 60 m (median = 13 m). Bull trout are coldwater tolerant fish; therefore it is not surprising that temperatures in Smith-Dorrien Creek rarely exceed 10°C even in the height of summer (see Chapter 2). As such, juvenile bull trout (age-1 and up) are inherently nocturnal feeders (Goetz 1997a), and the calculated home range should incorporate the nocturnal feeding range of the fish.

Smith-Dorrien Creek is dominated by juvenile bull trout but also has a small population of resident adults. Over a 2-3 month period in the fall, it is inundated with large adfluvial adults moving upstream to spawn. Unlike other streams or species where the placement of juveniles is strictly regulated by inter/intraspecific interactions with larger adults, juvenile bull trout in Smith-Dorrien Creek appear to be able to develop home ranges that accommodate a balance between predation risk and the opportunity to assess quality of habitat over a distance while also maintaining a safe refuge. Of course, the presence of adults does play a role in the habitat use of juveniles, but the risks associated with adults may vary temporally. Juvenile bull trout move into shallower water when adfluvial bull trout adults move upstream to spawn and display an increased awareness of their surroundings (see Chapter 4), and resident bull trout adults have been observed to displace (and feed on) juveniles in a pool when they move in.

Juvenile bull trout showed fidelity to particular daytime refuges as indicated by the low number of refuges in comparison to nighttime feeding locations. High variability in feeding locations suggests that feeding habitat is not a limiting factor within the system. In Smith-Dorrien Creek fish could move large distances to feed, but return to the same refuge or “home stone”, suggesting that refuge habitat may be a more limiting factor worth returning to instead of finding a new refuge close to a feeding location. Refuge habitat, especially during the winter has been hypothesized to be a limiting factor for salmonids (Thurrow 1997; Harwood et al. 2002). The temperature regime in Smith-Dorrien Creek is below the point where salmonids generally move from diurnal to nocturnal activity and seek out daytime refuges, which for many fish species in more temperate climates is at the onset of winter. Seasonal habitat shifts are common in

salmonids associated with changes in behaviour, habitat use and location during the transition from late summer to early winter (Northcote 1992). Cutthroat trout (*Oncorhynchus clarki*) in a coldwater Wyoming stream with a temperature regime throughout the season that was at or below the range where behavioural changes occur, did not move to new habitat when temperatures continued to drop (Young 1998). These fish maintained home ranges year round that provided suitable winter habitat and cover, not unlike juvenile bull trout in Smith-Dorrien Creek.

Habitat preference of juvenile bull trout in Smith-Dorrien Creek is consistent with findings from other bull trout streams (Baxter and McPhail 1997; Goetz 1997b; Thurow 1997; Watson and Hillman 1997; Bonneau and Scarnecchia 1998). Pools and runs were used more and riffles less than expected based on availability. Cobble and boulder substrate was the dominant choice for daytime refuge and was more common in habitat units used during the day compared to the night. Cover provided by cobble substrate provides protection from predators and reduces energy expenditure during the day by providing a velocity refuge (Harwood et al. 2002). Suitable cover can become increasingly important during the winter. Cobble substrate can provide protection against physical damage from ice moving in the water column (Harwood et al. 2002).

Home ranges of juvenile bull trout are variable in size and the determination of their extent depends on the temporal sampling regime. With a nocturnally active species such as bull trout, the home range may be extremely small if measured on a weekly basis during the daytime. Measuring bull trout movement at night indicates that movement in the stream can be dramatically greater than was previously suspected. Daytime measurements are still extremely valuable because they provide information on the

overall displacement of a fish and identify key refuges that juvenile bull trout prefer.

Variation in temporal scale also provides information on seasonal variation in habitat use and movement. Habitat information collected from both day and night use indicates the importance of pools, runs and cobble/boulder substrate as key habitat characteristics for juvenile bull trout. A limitation in this study was that nighttime measurements of radio-tagged fish were conducted during a short time interval after dusk. Limited data collected and literature from other species indicate that movement can occur throughout the night and the overall range of movement measured during this study is likely an underestimate of actual ranges. Estimates of the composition of mobile and sedentary bull trout in Smith-Dorrien Creek assume that the high proportion of fish that were never captured again had moved out of the study sections. This study addressed the concerns noted in past studies of edge effects associated with small study sections but did not address the ability to determine the extent of fish movement outside of the study section. A combination of large study sections with either weir traps at the upper and lower boundary, or PIT tag scanners at confined exits to each section would allow a more definite determination of the range of movement. Use of radio tags allowed some determination of the actual extent of movement, but tag size limits use to fish  $> 150$  mm, cost limits sample size and the small size of the tags limits the life of the battery.

Table 3.1 Summary of telemetry tag deployment and fish characteristics. Actual number of tags used in analysis (in parentheses) was lower as two tags died within five days of deployment and two tags showed no movement throughout the life of the tag and is suspected that these fish died or the tags were shed.

Date	Number of Tags Applied (Used)	Mean Fish Size (Range)	Stream Section	Frequency of Assessment
Aug 6 – Aug 21 1998	6 (5)	175.8 mm (163 – 197 mm)	3 in section 2 and 3 in section 3	Day and Night
Sep 9 – Sep 27 1998	5(4)	171.2 mm (164 – 185 mm)	3 in section 2 and 2 in section 3	Daily (not used in day to night movement comparisons)
July 6 – July 28 1999	10	173.9 mm (160 – 193 mm)	5 each in sections 2 and 3	Day and Night
Aug 19 – Sep 9 1999	10 (8)	164 mm (157 – 189 mm)	5 each in sections 2 and 3	Day and Night
Sep 15 – Oct 6 1999	8	158.4 mm (151 – 171 mm)	4 each in sections 2 and 3	Day and Night
Total	39 (35)			

Table 3.2 Numbers of bull trout in each sample cohort (bold) and number known to be alive/present in study section after initial capture. Each sample cohort represents untagged fish captured within a particular sample event. Recapture values from a total of nine sampling events after first capture were used to calculate capture efficiency. Shaded area shows continuation of data for each sampling cohort beyond the ten sample sessions used for analysis.

Date Cohort	1998										1999								
	05/05	21/05	06/06	11/06	06/07	27/07	26/08	14/09	06/10	26/10	05/05	13/05	02/06	29/06	22/07	26/08	13/09	20/09	27/10
1	<b>76</b>	26	21	19	16	13	8	4	3	2	1	1	0	0	0	0	0	0	0
2		<b>102</b>	53	46	44	33	18	12	8	6	3	3	1	1	1	0	0	0	0
3			<b>52</b>	31	30	23	16	9	7	5	4	4	4	2	1	0	0	0	0
4				<b>79</b>	45	32	21	13	10	8	7	5	4	4	1	1	1	1	1
5					<b>91</b>	31	23	15	14	11	7	7	5	3	3	1	1	1	0
6						<b>156</b>	57	40	30	26	18	14	11	9	8	5	2	2	2
7							<b>154</b>	35	31	30	25	23	20	15	13	8	6	3	2
8								<b>78</b>	22	17	14	13	11	10	10	6	6	4	1
9									<b>72</b>	28	15	13	11	9	8	5	3	3	0
10										<b>93</b>	37	32	24	23	22	18	14	7	3

Table 3.3 Radio-tagged fish grouped with respect to movement (range < or > 50 m), overall displacement (< or > 50 m), and fidelity to daytime refuges (low > 4, high ≤ 4). The combination of low movement and high displacement is not possible as displacement cannot exceed movement. Fish with high movement, high displacement and high fidelity are generally fish that showed low movement and displacement within the stream and then migrated downstream to Lower Kananaskis Lake.

<b>Movement</b>	<b>Low</b>	<b>High</b>	<b>Low</b>	<b>High</b>
<b>Displacement</b>	<b>Low</b>	<b>Low</b>	<b>High</b>	<b>High</b>
<b>High Fidelity</b>	16	3	-	5
<b>Low Fidelity</b>	6	0	-	5



Table 3.4 Summary statistics of chi-square tests on various habitat variables between day and night. Critical P value is 0.05.

Test	Chi square Value	df	P
Substrate composition within:			
Runs	12.03	2	0.002
Pools	24.46	2	< 0.0001
Riffles	2.95	2	0.023
Cover available within:			
Runs	34.93	3	< 0.0001
Pools	13.90	3	0.003
Riffles	1.83	3	0.61
Stream velocities at:			
Substrate	0.02	2	0.99
0.6 depth (mean flow)	0.04	2	0.98
Surface	0.12	2	0.94

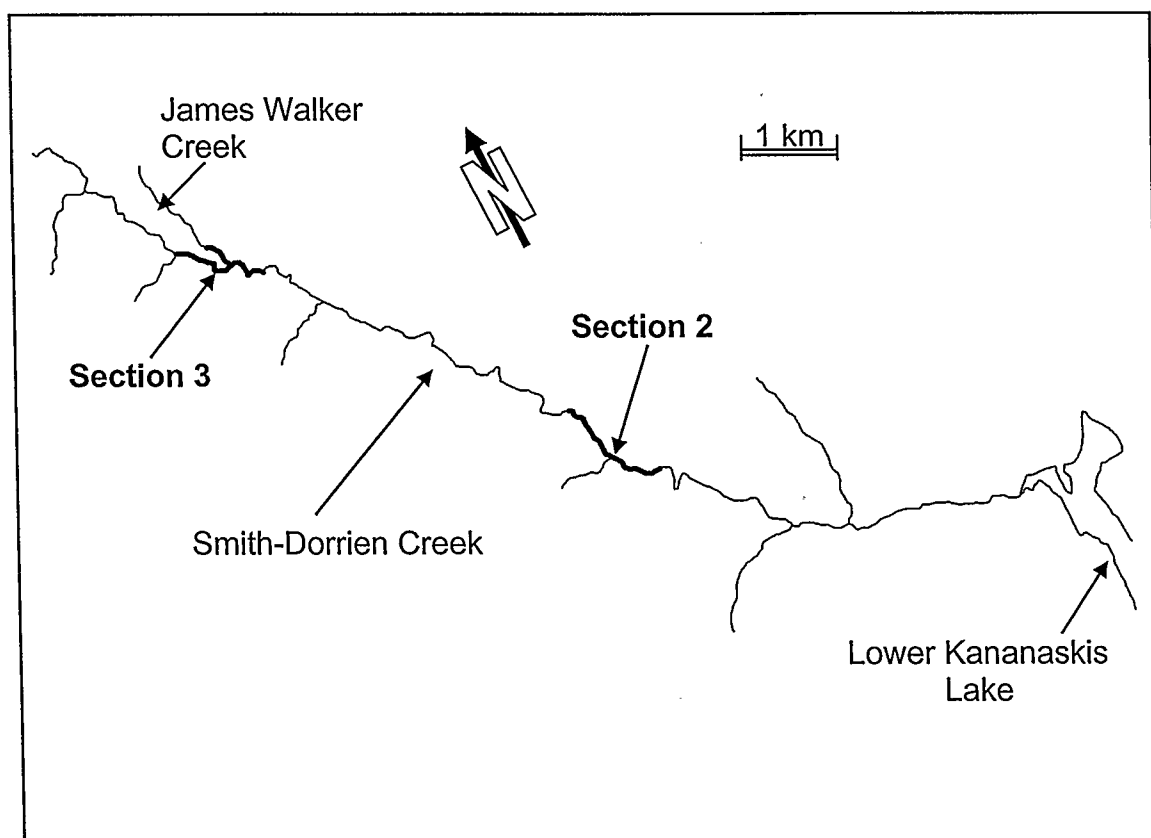


Figure 3.1 Map of Smith-Dorrien Creek indicating locations of study sections 2 and 3.

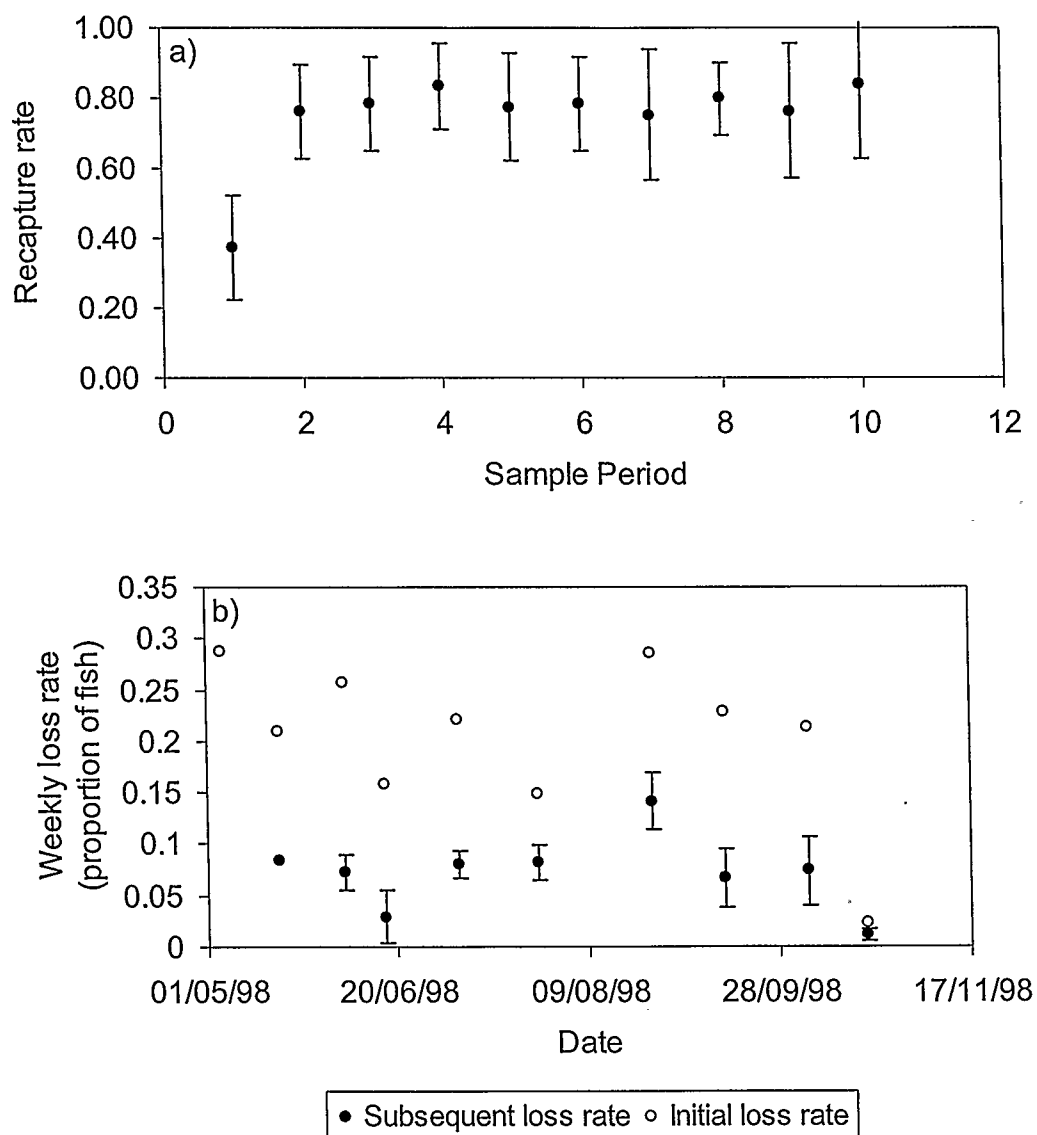


Figure 3.2 a) Recapture rates of 10 sampling "cohorts" from the first recapture after initial tagging to the final sampling (total of 10 sampling periods). Each sample period is the corresponding sequential recapture period of each of the 10 cohorts. For example, sample period 1 contains the first recapture session of all 10 cohorts which vary in time depending on when each cohort was established (see Table 3.1). Error bars are standard deviation (SD). b) Weekly loss rate (proportion of fish lost between sample periods) of PIT-tagged bull trout throughout the 1998 sampling season. The last set of data points show low loss rate from late October 1998 to May 1999. Data are divided into two groups: open circles are migration after first capture (only one data point per date) and solid circles are the mean migration rate of all sampling "cohorts" active within a time period with SD error bars. Migration rates are highest for fish within the first time period after tagging.

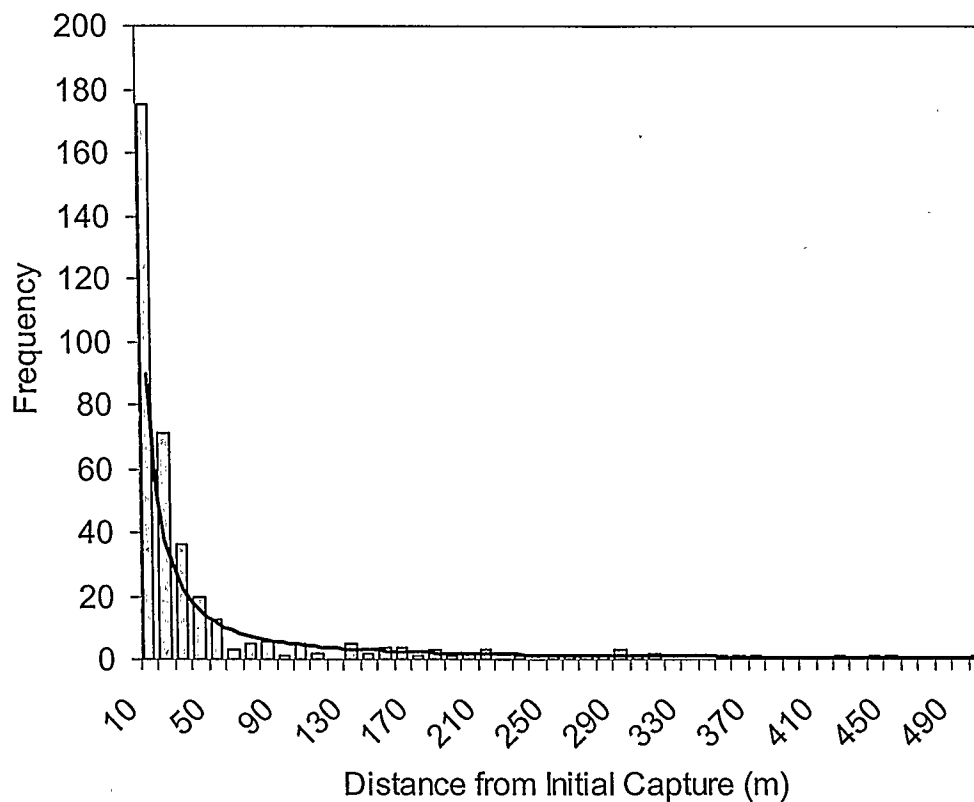


Figure 3.3 Frequency histogram of juvenile PIT-tagged bull trout and their distance from the initial point of capture for all data from 1998 and 1999. Distance bins are in 10 m intervals with the number indicated representing the upper limit of the bin. This figure was truncated at 500 m which contains 96% of all fish. Maximum distance measured by fish not migrating into Lower Kananaskis Lake was 4800 m. Solid line indicates a negative power relationship ( $y = 89.8 x^{-1.3}$ ,  $R^2 = 0.82$ ).

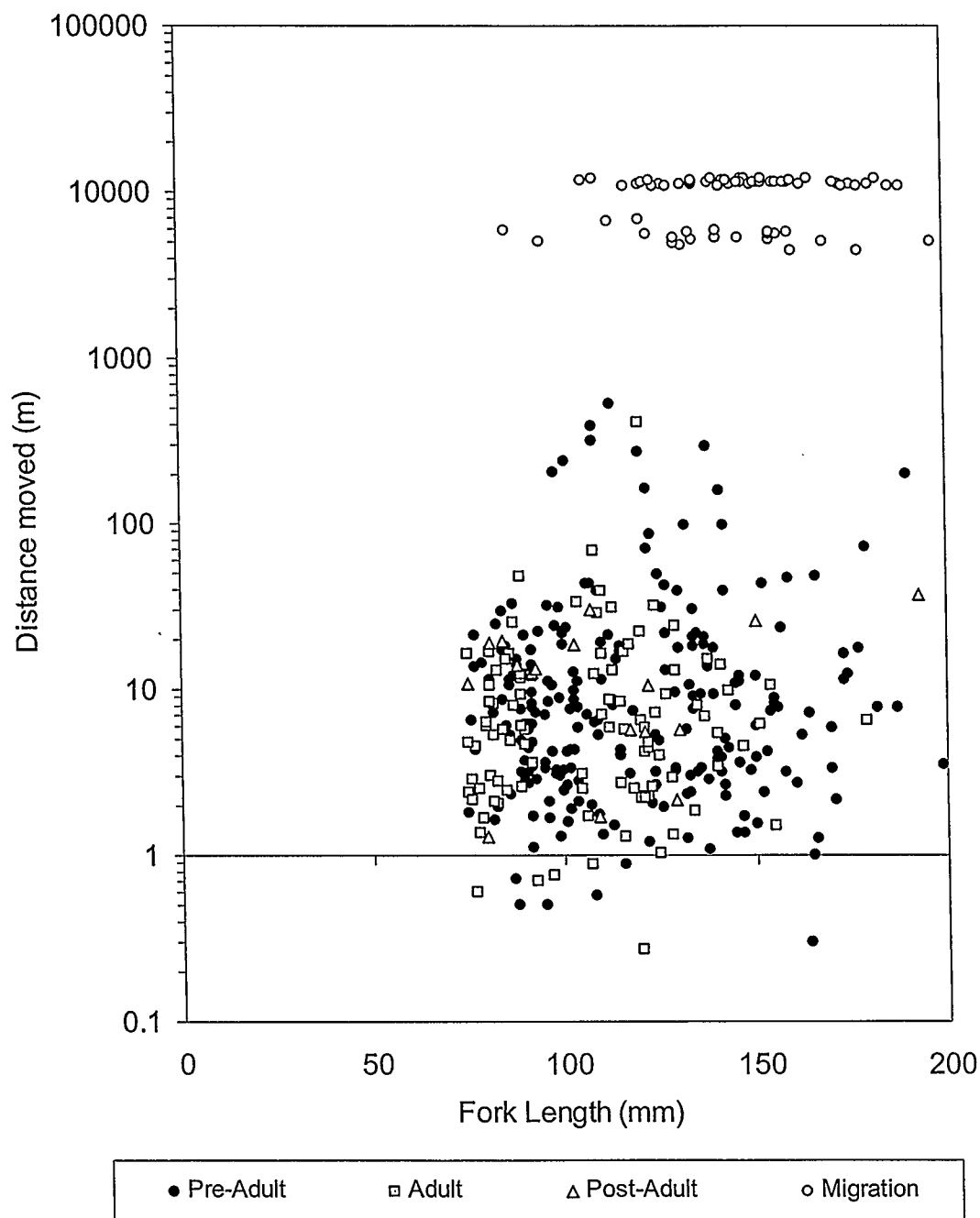


Figure 3.4 Overall distance moved within a 40-day period of PIT-tagged juvenile bull trout in relation to fork length of tagged fish. Data are separated into four groups: pre-adult (May-August), adult (August-October), post-adult (October), and migration (movement out of Smith-Dorrien Creek). There was no significant difference in distance moved with respect to size or to time period (except for migration). Note y-axis is on a logarithmic scale and no fish smaller than 75 mm in length received a PIT tag.

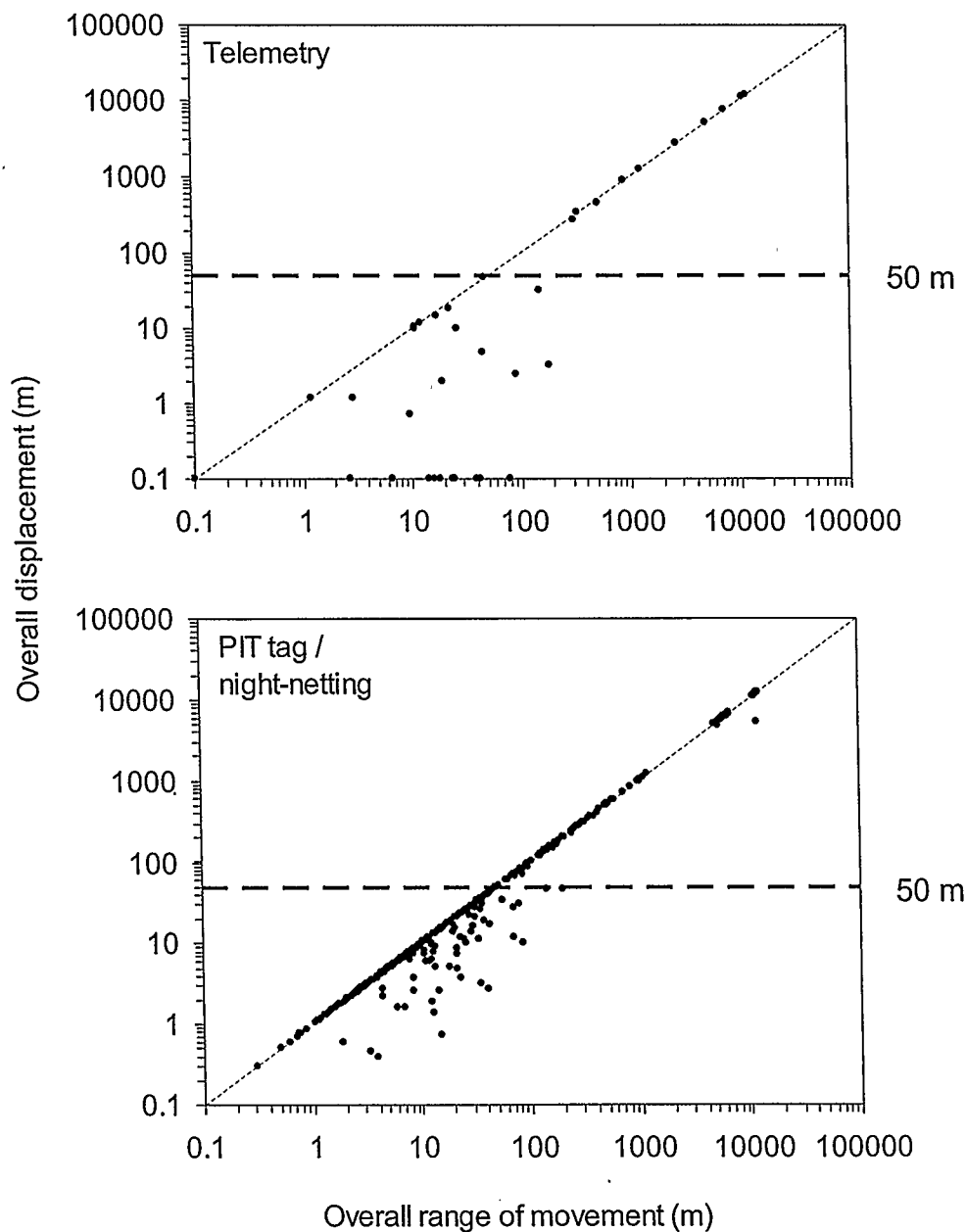


Figure 3.5 Comparison of overall range of movement of juvenile bull trout to overall displacement for radio-tagged (time scale < 22 days) and PIT tagged fish (time scale > 25 days). Overall range encompasses the distance between the most upstream and downstream locations that an individual fish was captured. Overall displacement is the distance between the point of capture and the final location where the individual fish was captured. Note axes are on a logarithmic scale, light dashed line indicates 1:1 line and heavy dashed line indicates 50 m displacement. Points on the 1:1 line indicate fish whose displacement equaled their range of movement. Points below the 1:1 line indicate fish that moved in both directions, reducing the overall displacement in comparison to the range.

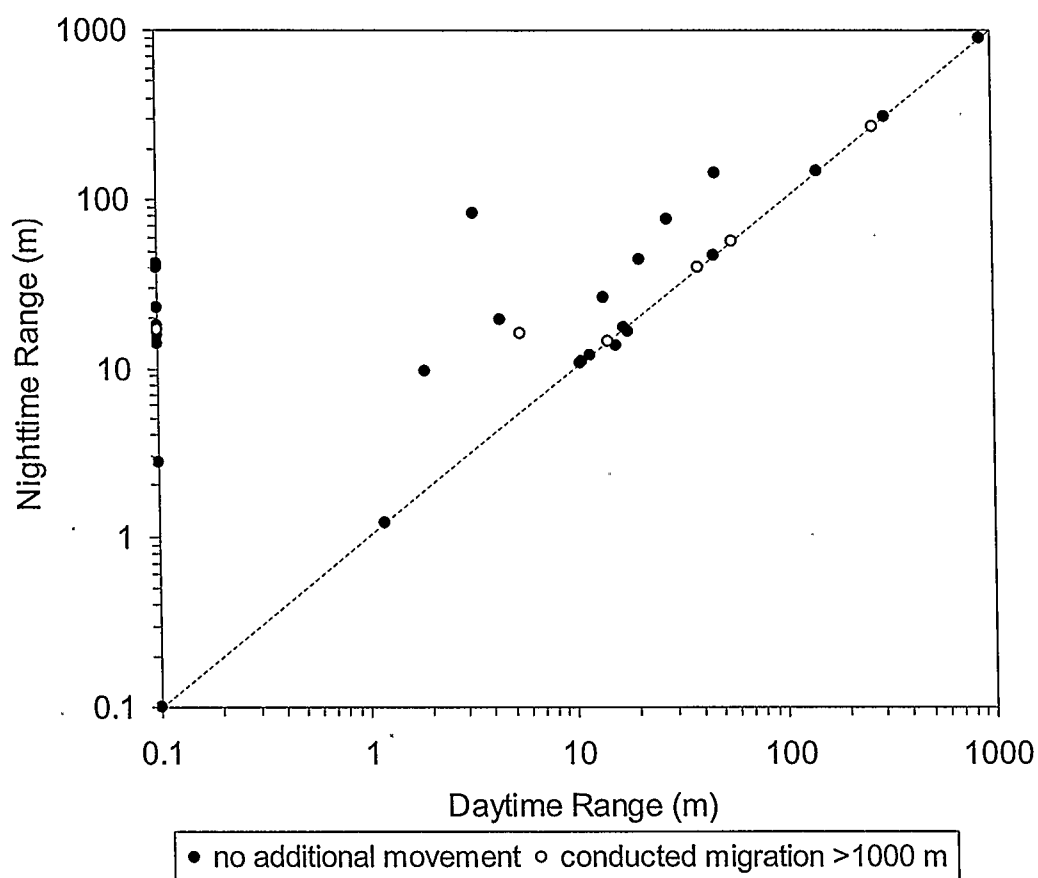


Figure 3.6 Relationship between nighttime range and daytime range for radio-tagged juvenile bull trout prior to downstream migration. Non-solid points indicate fish that eventually migrated downstream. Dashed line indicates 1:1 line. Note axes are on a logarithmic scale.

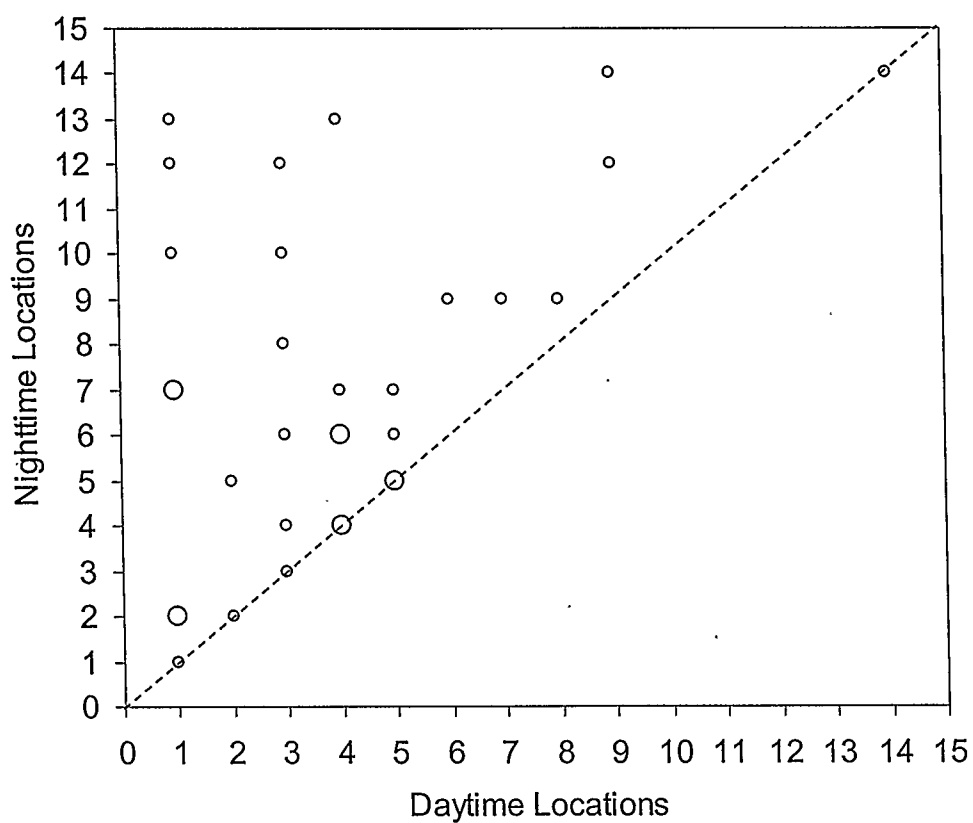


Figure 3.7 Relationship between number of nighttime and daytime locations identified for individual radio-tagged bull trout. Nighttime locations were either equal to or more numerous than daytime locations. Larger points represent two values at that point. Dashed line indicates 1:1 line.



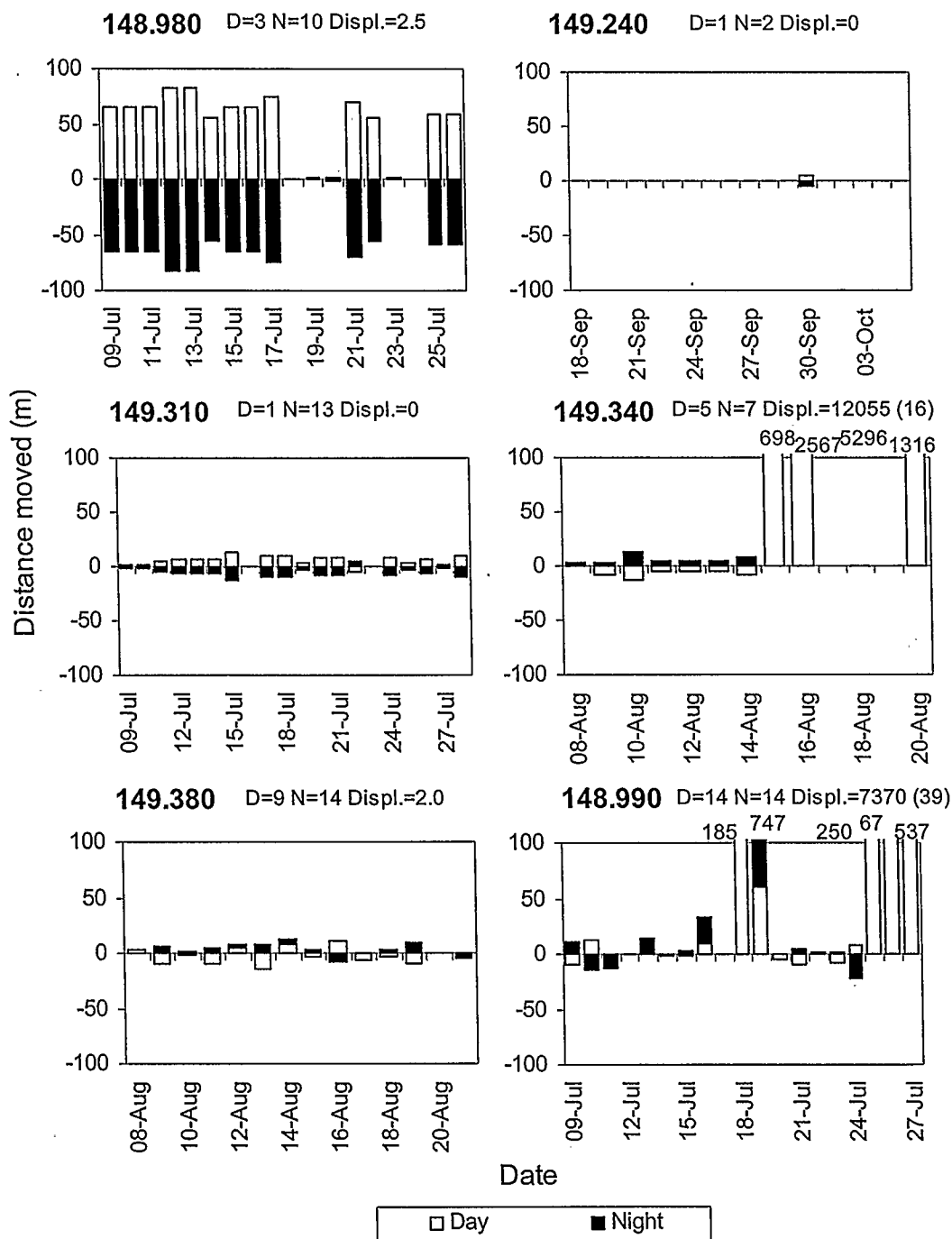


Figure 3.8 Selection of graphs outlining various diel movement behaviours of radio-tagged bull trout. Each graph is referenced by the telemetry tag number and is accompanied with an indication of the number of day (D) and night (N) locations and overall displacement (Displ.). Note x-axis scales vary and each graph encompasses the entire life of a radio-tag. Numbers in brackets indicate displacement before downstream migration.

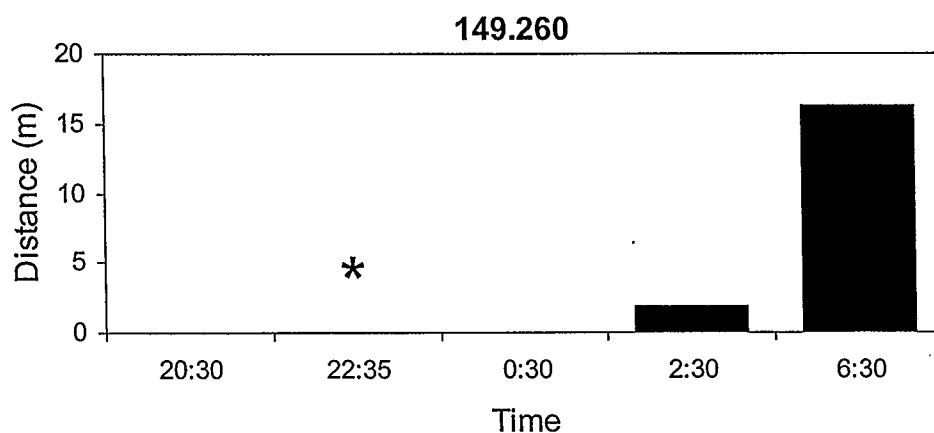


Figure 3.9 Distance radio-tagged fish 149.260 moved when checked at five time intervals throughout the night on 6 October, 1999. The first sample time (20:30) is before dusk when no movement is expected. The second time is just after dusk (\*). The fish was normally checked between the second and third time period (around 23:00). Subsequent times cover the rest of the night and show that the fish moved throughout the night and that an assessment of no movement at one time does not mean that the fish does not move out to feed at a later time. The fish returned to the same daytime refuge at dawn.

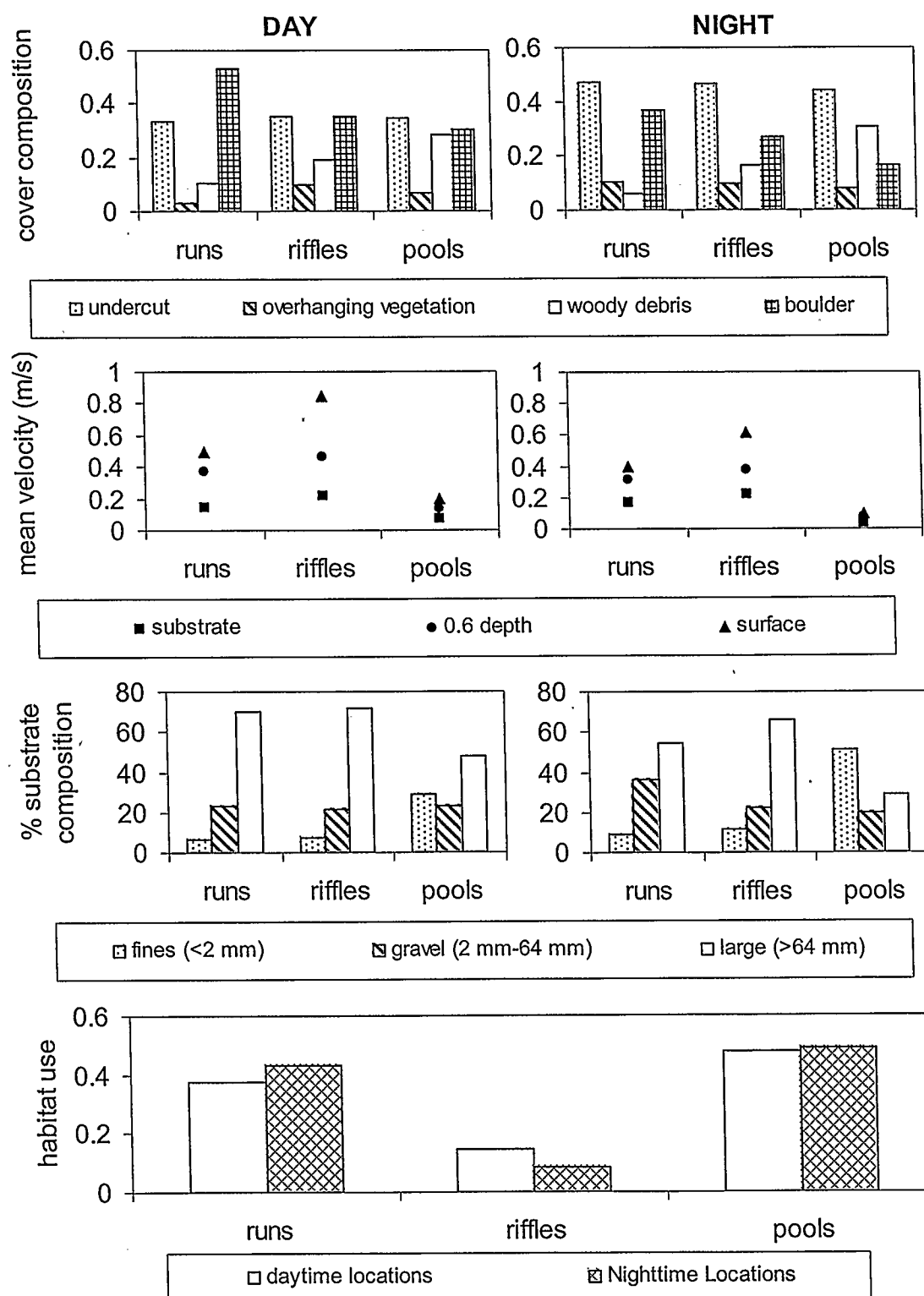


Figure 3.10 Comparison of habitat variables measured between day and night for 35 radio-tagged bull trout. Variables include cover types, stream velocity, substrate composition and stream habitat units.

## Chapter 4 – Effect of adult presence on juvenile behaviour and habitat use

### 4.1 Introduction

Defining habitat requirements of fish is a necessary first step towards identifying and protecting critical habitat features (Rosenfeld and Boss 2001), and is of key interest in the adoption and successful implementation of the Alberta bull trout management and recovery plan (Berry 1997). The habitat requirements of mobile life stages of fish are typically inferred from field surveys, documenting the selection of different habitats in which selection is measured in terms of differential use or occupancy of particular habitats (Rosenfeld and Boss 2001). Habitat use in the wild may not reflect habitat preference in the absence of biotic interactions, particularly for juvenile fish, which may be forced into suboptimal habitats by competition or predation (Werner and Hall 1988; Landry et al. 1999). Interference competition, involving aggressive interactions among individuals that preempts resources, favours larger individuals and forces smaller ones into less profitable habitats (Grant 1990).

Competitive interactions between and within species can have a profound effect on growth, survival and density within an environment (Post et al. 1999). Competing individuals or species may segregate spatially or temporally to reduce the intensity of interactions. For example, coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) segregate spatially by coho residing in pools and steelhead in riffles as a result of active behavioural interactions (Hartman 1965). Competition for food is not completely eliminated, but certainly reduced by such spatial differentiation. Territorial fish species regulate their territory size based on food availability and ability to defend a territory.

Successful territorial fish grow more rapidly than subordinates, and aggressive behaviour appears to be a key factor in causing downstream drift of coho salmon (Chapman 1962). Food abundance may vary over time and territorial species must ensure that the minimum territory size is enough to maintain the individual when food resources are low. Chapman (1966) demonstrated that many stream fish reduce aggression and tolerate contemporaries at closer range if food is temporarily abundant.

In addition to interference competition through territorial behaviour, the risk of predation can also influence habitat and food selection (Werner et al. 1983a, 1983b; Gilliam and Fraser 1987). Numerous studies, especially in lentic systems, have demonstrated the adaptive behaviour of fish to weigh the benefits of habitat profitability against predation risk (Werner et al. 1983; Mittelbach 1986; Tabor and Wurtsbaugh 1991; Landry et al. 1999). In many cases, the pelagic zone of lakes is the most profitable habitat with respect to food (Werner et al. 1983; Tabor and Wurtsbaugh 1991), but the presence of predatory individuals forces smaller fish into the less profitable, but less risky, littoral zone (Tabor and Wurtsbaugh 1991; Post et al. 1998, 1999). In the absence of predators, these smaller fish maximize their energy intake and growth rates by using the most profitable habitat (Landry et al. 1999). In the presence of predators, smaller fish may still venture out into the open water during periods of reduced risk, such as under the cover of darkness (Landry et al. 1999). Small fish face a trade-off between risk of cannibalism and habitat-specific prey profitability (Gilliam and Fraser 1987), but the trade-off changes through ontogeny as the young fish grow (Miller et al. 1988). Landry et al. (1999) found that in a lake containing only age-0 rainbow trout (*Oncorhynchus mykiss*), these trout used the more profitable pelagic zone. When adult rainbow trout

were added partway through the season, there was a shift in the habitat use and diet of many young fish, which had not undergone ontogeny, towards nearshore habitat.

In the Lower Kananaskis Lake / Smith-Dorrien Creek system, adult bull trout move up Smith-Dorrien Creek to spawn (Stelfox 1997; Chapter 2). Shortly after the entry of adults into the creek, I have noted a downstream migration of juvenile bull trout. Although environmental variables likely play a role in the choice of juveniles to move downstream, I have also shown that the downstream migration consistently occurs one to two weeks after the entry of adults into the stream (Chapter 2). Adult bull trout are piscivorous (Stelfox 1997; Mushens et al. 2003), and adults can prey on juveniles during the upstream migration (Mushens et al. 2003). During the upstream migration, these adult bull trout will hold in deeper pools and runs within the creek to minimize exposure and predation risk themselves. I hypothesize that the presence of these potential cannibals will affect the behaviour and habitat use of juveniles. Not unlike rainbow trout in lentic systems, the juvenile bull trout may be required to move into sub-optimal or shallower habitat or to migrate out of their stream rearing habitat, to minimize encounters with much larger and potentially cannibalistic conspecifics. To determine whether juvenile bull trout alter habitat use while adults were present within the creek, I captured juvenile bull trout throughout the season from May to October in 1998 and 1999, and measured the depth of habitat used. I predicted that juvenile bull trout would use shallower habitat when adults were present in the stream, when compared to sampling periods both before and after the presence of adults. In 1999 I also quantified the behaviour of juvenile bull trout by determining the capture efficiency during sampling, which I argue provides an index of vigilance. I predict that juvenile bull trout should be

more vigilant (lower capture efficiency), when adults were present in Smith-Dorrien Creek than before the adult upstream migration.

## **4.2 Methods**

### **4.2.1 Study Area**

In 1998 and 1999, two sections of Smith-Dorrien Creek and a small tributary were surveyed for juvenile bull trout. The first section (Section 2) is 1580 m in length and is located 4.3 km upstream from Lower Kananaskis Lake (Figure 4.1). Section 3 is 4.7 km upstream of Section 2 and is 1260 m in length. James Walker Creek (JWC), a small tributary, enters Smith-Dorrien Creek 320 m upstream of the lower boundary of Section 3. The section of JWC that was sampled was 265 m in length and blocked at the upstream end by an impassable beaver dam. Substrate in Section 2 was primarily cobble and channel structure was relatively consistent throughout the section with long straight runs and riffles (Table 4.1). Section 3 was much more variable. It contained numerous pools interspersed between riffle and run habitat. Substrate was comprised of primarily cobbles and gravels.

### **4.2.2 Field Technique**

Sampling occurred approximately every three weeks from May through October in both years. In 1998 sections 2, 3 and JWC were each sampled ten times. In 1999, nine sampling sessions were conducted.

Juvenile bull trout in Smith-Dorrien Creek are active at night and seek refuge during the daytime (Chapter 3). All sampling occurred from one hour after sunset until the section was completed or dawn, whichever came first. If a section was not completed in one night, it was finished the following night from the point where the previous night left off.

Fish were captured by night netting, a technique adapted from Bonneau et al. (1996). This consisted of walking upstream with halogen dive lights until an individual fish is spotlighted. Once a fish is located a dip net (0.6 mm dark-green mesh with an opening of 0.2 X 0.6 m) is placed 0.2 m downstream of the fish. The fish is then coaxed into the dip net from upstream using a rigid nylon sieve attached to a pole. Each bull trout was mildly anaesthetized (tricaine methane sulfonate – MS 222), after which the fish was measured (nearest 1 mm) and then marked using Passive Integrated Transponder (PIT) tags (Prentice et al. 1990).

The location of each fish was measured using a GPS receiver at the time of capture. These coordinates were later differentially corrected using the base station located at Barrier Lake Field Station, University of Calgary. This permitted the accurate positioning of juvenile bull trout to within approximately one metre of its actual location. The depth of the water, habitat type (i.e. run, riffle, pool) and substrate composition using a simplified Wentworth scale (Nielson and Johnson 1993; Chapter 3) were also recorded with each measurement.

During the 1999 sampling season, I attempted to quantify the behaviour of fish with respect to vigilance. This was achieved by keeping count of the total number of individual bull trout seen during each sampling session and the total number of fish



caught on first attempt. Using experienced personnel, the dip net was consistently placed 0.2 m behind the subject. In some cases the subject would become wary of the presence and escape to either side of the net, constituting an unsuccessful attempt. With a period of approximately three weeks passing between sampling sessions, I assume that previously tagged fish would not show an increase in wariness. If this was not true, I would expect that sampling sessions that had a higher proportion of tagged fish would also display higher occurrences of unsuccessful first attempts. Because Section 3 and JWC were sampled concurrently, no differentiation in capture efficiency between the two sections is possible.

#### **4.2.3 Analysis**

For both years, data for sections 2, 3 and JWC were analyzed separately unless otherwise stated. I assume that larger individuals prefer deeper habitat than smaller individuals. As fish grow throughout the season, I would predict that fish would be found in deeper water as permitted by the channel structure.

I used a three way analysis of covariance (ANCOVA) to test the hypothesis that depth use of juvenile bull trout differed with the presence of adults. The three treatments were year (1998 and 1999), adult presence which was grouped into three levels: pre-adult, adults present and post-adult, and study section also grouped into three levels (section 2, 3 and JWC). Replicates within each level were depths used by individual fish. Depth data were log transformed to satisfy the assumption of normality. As mentioned above, larger fish are assumed to use deeper habitat than smaller fish. As the size

frequency distribution may vary between samples, fork length of fish at each depth was also included as a covariate. By including fork length as a covariate I can reduce the amount of unexplained variance due to size, thereby decreasing the value of  $MS_{\text{between}}$  leading to a larger F statistic.

I predicted that juvenile bull trout will shift their habitat use to shallower sites during the period when adults are present in the stream compared to both before and after adult presence. Data from JWC permit a presence / absence experimental design. In 1998 when adults spawned in JWC, I predicted that juvenile depth use would decline with adult presence, but in 1999 there should be no difference in depth use over the three periods as adults were not present in JWC. Comparisons within treatments were conducted with a one way ANCOVA with the Bonfferoni correction applied to  $P_{\text{crit}}$  (Sokal and Rohlf 1995).

The second goal of this study was to quantify the ability of juvenile bull trout to assess risk through an index of vigilance. The index of vigilance is inversely related to the calculation of capture efficiency for each sample session in 1999:

$$CE = \frac{n_{\text{cap}}}{n_{\text{obs}}} \quad (4.1)$$

where capture efficiency ( $CE$ ) equals the proportion of the number of fish that were successfully caught on first attempt ( $n_{\text{cap}}$ ) and the total number of fish seen ( $n_{\text{obs}}$ ).

Therefore, I propose the index of vigilance ( $V$ ) as:

$$V = 1 - CE \quad (4.2)$$

The index of vigilance will range from zero to one with one equating to maximally wary fish that elicit an escape response at the first sign of disturbance. I used a two way

ANCOVA to determine whether vigilance increased when adults were present in the stream. Treatments were adults (present or not present) and study section (section 2 or 3). Replicates were capture efficiency measured from each sample event. Because only one data point was collected for the time period after adults were present in the system, data were separated into two time period categories: adults present and adults not present (before and after). Because no differentiation was made between capture efficiency in Section 3 and JWC (see field technique), data for Section 3 includes fish from JWC. To determine the possible effect that an environmental factor such as moon phase may have on the behaviour of juveniles, moon phase was included as a covariate. Moon phase was a continuous variable with a numerical value assigned to the day in the moon cycle. A new moon was assigned a value of 1, and values each day increased with the waxing moon up to 15 for full moon and then declined back to 1 with the waning moon. No information on cloud cover was collected.

## **4.3 Results**

### **4.3.1 Habitat Depth Use**

Juvenile bull trout in Section 2 maintained an average habitat depth between 0.18 and 0.25 m in 1998 and 0.19 and 0.28 m in 1999, during 5-6 time periods prior to the movement of adults into Smith-Dorrien Creek (Figure 4.2). After adults entered the creek, mean depth declined to between 0.12 and 0.17 m in both years. Once adults had left the creek in early October, juveniles were found inhabiting deeper water once again. Similar trends are observed for bull trout in Section 3. Depth use prior to adult presence

was around 0.3 m and declined to below 0.2 m once adults had entered the creek. In 1999, the sixth sampling period occurred very shortly after adults had entered Smith-Dorrien Creek. Although depth use declined in Section 2 during this sampling, Section 3, which is located further upstream, did not show any difference in mean depth from previous sessions. This suggests that adult bull trout had not moved upstream into Section 3 by that time. The subsequent sampling periods in section 3 do indicate a sharp decline in depth. Once again, as for Section 2, depth use increased after adults had moved back to the lake. Mean depth use in James Walker Creek (JWC), was a lot more variable throughout the season, and was probably affected by lower sample sizes in this short section of creek. The important point to note is that in 1998, depth use was generally above 0.2 m prior to adults, but did decline to below 0.2 m when adults moved in to spawn. In 1999, adults did not move into JWC and mean depth use remained consistently above 0.2 m throughout the season.

In both years in both section 2 and 3, the log of habitat depth use was significantly lower during the time period when adults were present in the creek (Figure 4.3, Table 4.2). There was also a significant positive relationship between fork length and log depth use, supporting the fact that larger fish used deeper habitat. In James Walker Creek, juveniles did use shallower habitat when adults were present in 1998, but in 1999 there was no significant change in log depth use while adults were present in Smith-Dorrien Creek but not in JWC. There was a significant year effect on log depth use in each study section and during each adult presence treatment. This indicates that environmental variables such as water level likely affect available depths each year.

Daily discharge in Smith-Dorrien Creek from late-July through October follows a steadily decreasing trend from 3 to 0.5 m<sup>3</sup>·s<sup>-1</sup> in 1998 and 4 to 1 m<sup>3</sup>·s<sup>-1</sup> in 1999 (Figure 4.4). Available depths within the stream are assumed to follow a similar decreasing trend. With this in mind, juveniles use deeper depths in October, after adults have left the system, suggesting that suitable depths are available throughout the spawning season also.

#### **4.3.2 Index of Vigilance**

Measurements of vigilance in Smith-Dorrien Creek in 1999 for sections 2 and 3 reveal the opposite trend as compared to depth use. Prior to adults moving into Smith-Dorrien Creek, vigilance values were low, with only 15 - 26 percent of juveniles in Section 2 attempting to evade capture (Figure 4.5). In Section 3, juveniles were even more docile with only 13 - 19 percent being missed. Once adults had moved into the creek, vigilance increased substantially. In Section 2, 40 - 50 percent of all juveniles displayed evasive behaviour. In Section 3, vigilance did not increase during the first sampling session that occurred very shortly after adults had entered Smith-Dorrien Creek. This supports the suggestion that adults had not yet reached this upper section of the creek. For the following two sampling sessions though, juvenile awareness was heightened and ranged between 25 - 27 percent. As predicted, once adults had moved back to the lake, juveniles were much easier to capture in both sections. In both sections, juvenile vigilance was significantly higher while adults were present in the creek as compared to the periods before or after adults (Table 4.3). Light intensity has often been

associated with the behaviour of fish. Periods of high light intensity are considered to increase predation risk, leading to increased vigilance of potential prey items, such as juvenile bull trout. In this case, increases in vigilance were not related to increased light intensity associated with the covariate moon phase (Table 4.3). Therefore the environmental variable moon phase was considered not to be a factor in the vigilance levels observed.

#### 4.4 Discussion

The results shown here suggest that juvenile bull trout alter their spatial behaviour and level of vigilance when adult bull trout enter rearing streams to reproduce. They move into shallower water and increase their level of vigilance. An alternate theory would be that the decrease in depths used by juvenile bull trout over time is associated with decreasing flows in Smith-Dorrien Creek. Depth use data for the time period after adults had left the creek indicates that this is not the case and suitable depths are available to juvenile bull trout throughout the spawning season. In Hudson Creek, B.C., cutthroat trout (*Oncorhynchus clarki*) segregate spatially based on intraspecific interactions (Rosenfeld and Boss 2001). Although pools were energetically more favourable for age-0, age-1 and age-2 fish, age-0 fish were forced to use riffle habitat in the presence of larger fish. In the absence of larger fish, age-0 fish selected pool habitat and had higher growth rates. Riffle habitat was energetically inefficient for larger fish. This situation is most likely prevalent within Smith-Dorrien Creek throughout the year, with larger juveniles using deeper pools and smaller bull trout using the marginal habitat. In fact,

age-0 bull trout segregate themselves from larger juveniles temporally, by having increased activity during the daytime and seeking refuge at night (Goetz 1997a). Based on energetic benefits alone, adult bull trout are expected to use pools and deeper runs while moving upstream to spawn each fall. Although this study looked at only intraspecific interactions, similar results have been observed with bull trout in interspecific interactions with brook trout (*Salvelinus fontinalis*). Nakano et al. (1998) found that bull trout exhibited reduced foraging distance and rate, and were associated with cover more often in the presence of brook trout than after brook trout were removed. After brook trout were removed, bull trout densities increased within the study area through immigration. This implies that brook trout can play an important role in regulating bull trout densities. Therefore, the introduction of competitive individuals, such as brook trout or adult bull trout, would be expected to lead to a decrease in the density of juvenile bull trout.

I suspect that juveniles did not alter their habitat use in 1992 when only 60 spawning adults were moving into Smith-Dorrien Creek but unfortunately no data are available to test this hypothesis. Encounter rate and predation risk would most likely have been very low. As observed in James Walker Creek in 1999, when adults did not move into the creek, juveniles did not alter their habitat use. The important factor to consider is that the adult bull trout population has increased from 60 adults in 1992, to 1370 in 2000. Adults feed on juveniles while moving upstream to spawn (Chapter 3) and with an average recruitment rate into the spawning population of around 450 fish each year (Mushens et al. 2003), juvenile bull trout may find themselves facing increasing predation risk each upcoming year.

An important question that has been asked in reference to the Lower Kananaskis Lake bull trout population is “what factors limit the growth of this population?” Of course, factors such as the carrying capacity of the lake for adults and Smith-Dorrien Creek for juveniles, as well as suitable spawning habitat are prime candidates. These factors are limited by physical geography, resource availability and intraspecific interactions within age-class groups (adults, juveniles, etc.). Intraspecific interactions between age-class groups may also play a key role in limiting bull trout numbers. I propose that as adult spawner densities increase, encounter rates with juveniles will increase, leading to a rise in the juvenile mortality rate as a result of cannibalism. This may create a negative feedback loop or bottleneck, limiting the number of juveniles that eventually migrate to the lake and mature after several years. Essentially, the adult spawners may be partially responsible for limiting the carrying capacity of the population by controlling juvenile numbers through cannibalism.

During the period of August and September, juvenile growth rates within Smith-Dorrien Creek decline as an effect of decreasing temperatures. As temperatures decline and food availability is reduced, territory size or foraging range would most likely increase to ensure sufficient nourishment (Slaney and Northcote 1974; Grant and Kramer 1990). In enclosure experiments during periods of high growth potential, juveniles of all ages experienced reduced growth at higher densities (Paul 2000). My data supports the hypothesis that the useable area for juvenile bull trout within Smith-Dorrien Creek decreases during the time period when adults enter the stream. During the fall, juvenile bull trout must not only be concerned with an increase in local density which may lead to a decline in growth rates, but also to the decline in food availability. Increased



interactions with conspecifics and limited foraging habitat will lead to some fish migrating downstream (Slaney and Northcote 1974). Juveniles must balance competition with other juveniles for food during times of declining resources while attempting to minimize potential predation risk.

To truly assess the effect that adults may have on juvenile habitat use and behaviour, an ideal experiment would be to block the entire creek below Section 3 to adult access. It has already been established that both Section 2 and Section 3 display similar results with respect to changes in depth use and vigilance, albeit with different values. Section 2 would be treated as a presence treatment and Section 3 as a treatment with the absence of adults. Although this experiment was essentially carried out in James Walker Creek, the conditions within James Walker were not completely controlled. The experiment in JWC was accidental, but fortuitous. Until 1998, it was not known that adult bull trout spawned in JWC. James Walker Creek is also a much shorter and narrower section of creek in comparison to Smith-Dorrien Creek and sample sizes were quite small. Repeating the experiment within the main channel of Smith-Dorrien Creek, would ensure sufficient sample sizes as well as a controlled environment with respect to adult presence.

Table 4.1      Habitat measurements of sections 2 and 3 of Smith-Dorrien Creek, and James Walker Creek (JWC). Depth and habitat unit composition data not collected for JWC.

Measurement	Section 2	Section 3	James Walker Creek
Length (m)	1580	1260	265
Mean Width (m)	10.4	7.8	4.3
Mean Max. Depth (m)	0.56	0.49	n/a
% Run	20	34	n/a
% Riffle	71	43	n/a
% Pool	9	23	n/a

Table 4.2 Results of 3 way analysis of covariance (ANCOVA) determining whether juvenile bull trout used shallower habitat (log depth), while adults were present in the stream (Adult Presence), compared to both before and after adults were present. To remove any bias of larger juveniles using deeper habitat, fork length was introduced as a covariate. Refer to Figure 4.3 for a graphical representation of these results.

Source	df	Mean-Square	F-Ratio	P
Year	1	2.03	41.41	< 0.0001
Adult Presence	2	4.37	88.94	< 0.0001
Section	2	1.67	34.01	< 0.0001
Year*Adult Presence	2	0.32	6.42	0.002
Year*Section	2	0.46	9.31	< 0.0001
Adult Presence*Section	4	0.15	2.99	0.018
Year*Adult Presence*Section	4	0.23	4.67	0.001
Fork Length	1	11.91	242.68	< 0.0001
Error	2312	0.05		

Table 4.3 Results of two way analysis of covariance (ANCOVA) determining whether vigilance of juvenile bull trout in sections 2 and 3 (include JWC), differed in response to the presence or absence of adult bull trout (see Figure 4.4) with moonlight intensity as a covariate.

Source	df	Mean-Square	F-Ratio	P
Adult Presence	1	0.13	65.03	< 0.0001
Section	1	0.05	25.16	< 0.0001
Adult Presence*Section	1	0.02	10.39	0.007
Moonlight Intensity	1	0.00	0.22	0.64
Error	13	0.002		

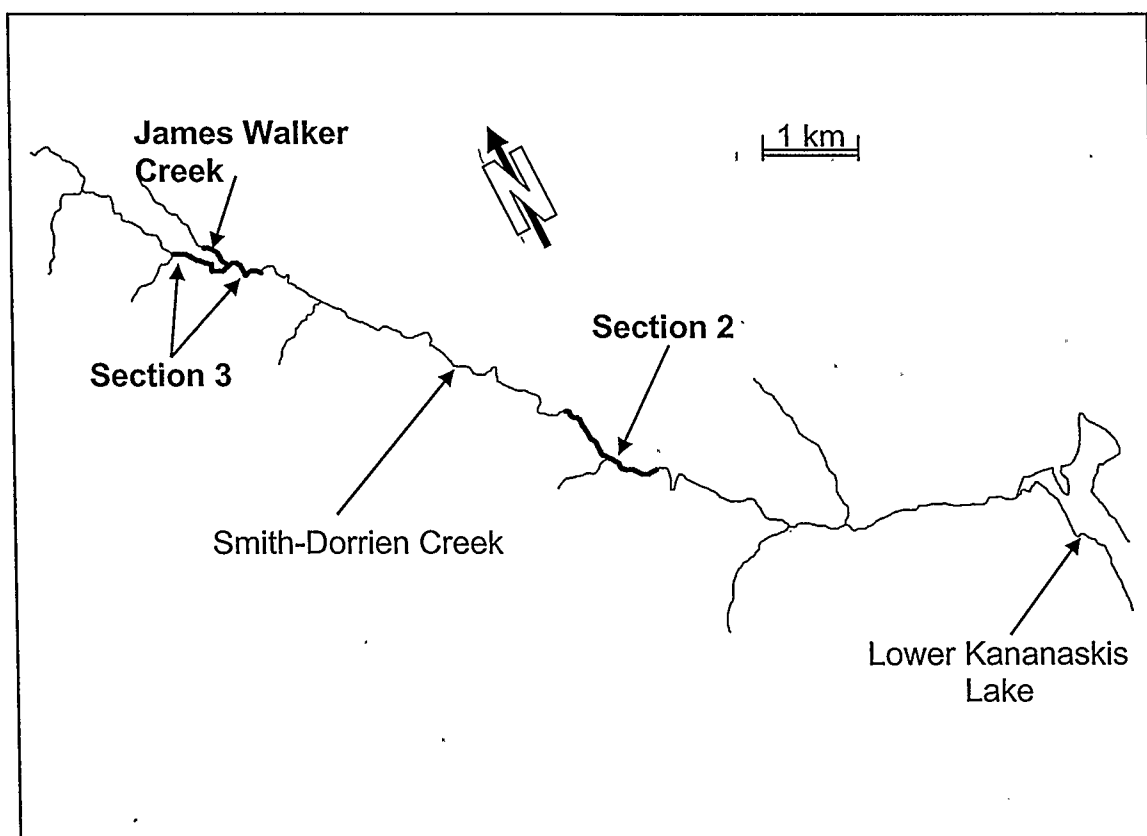


Figure 4.1 Map of Smith-Dorrien Creek indicating the location of the study sections 2 and 3, and James Walker Creek.

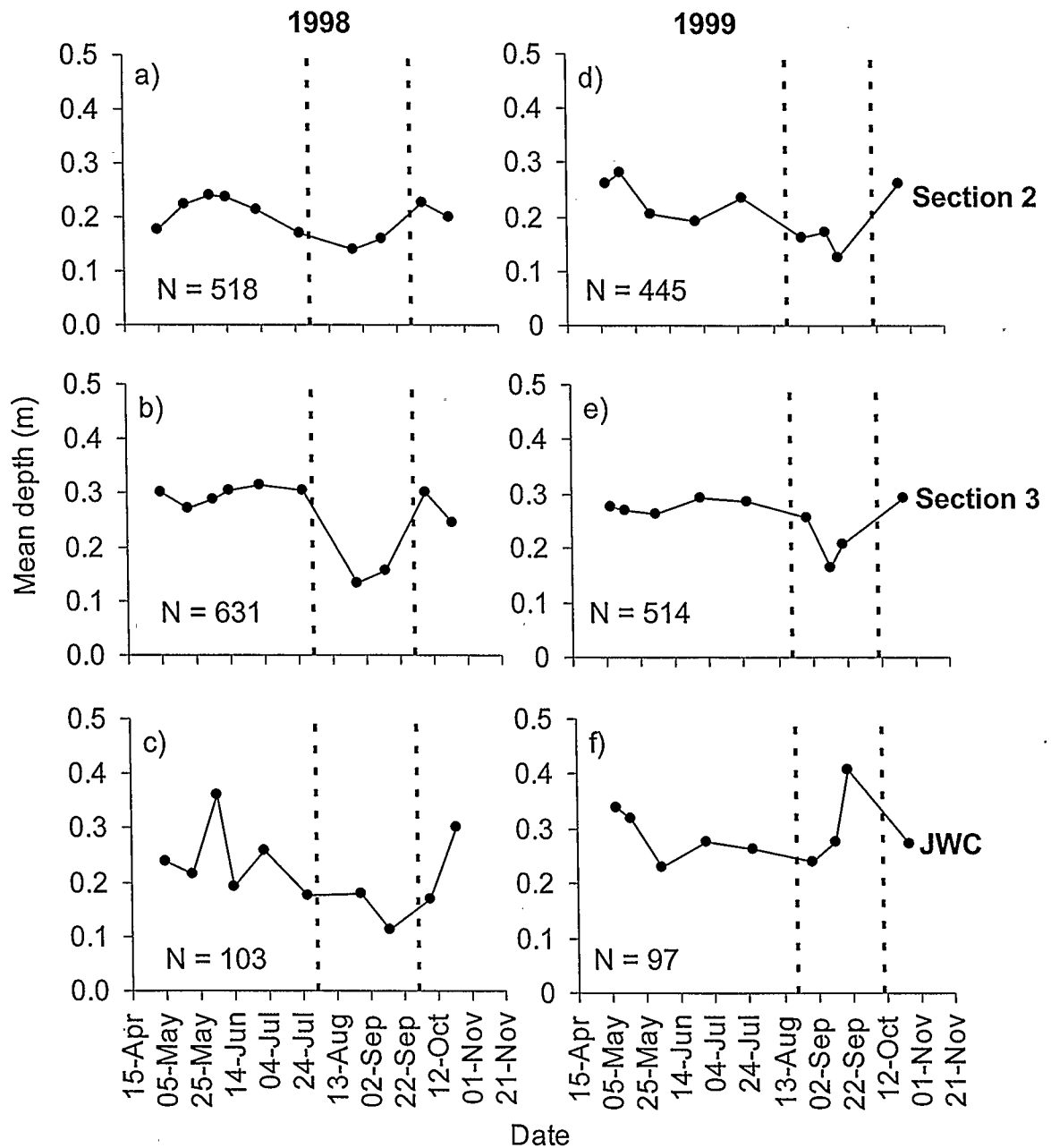


Figure 4.2 Mean depth use of juvenile bull trout in Smith-Dorrien Creek for each sampling date in 1998 (a - c), and 1999 (d - f), in all three study sections: Section 2 (a and d), Section 3 (b and e) and JWC (c and f). Area between the dashed vertical lines indicates the time period when adults were present in Smith-Dorrien Creek.

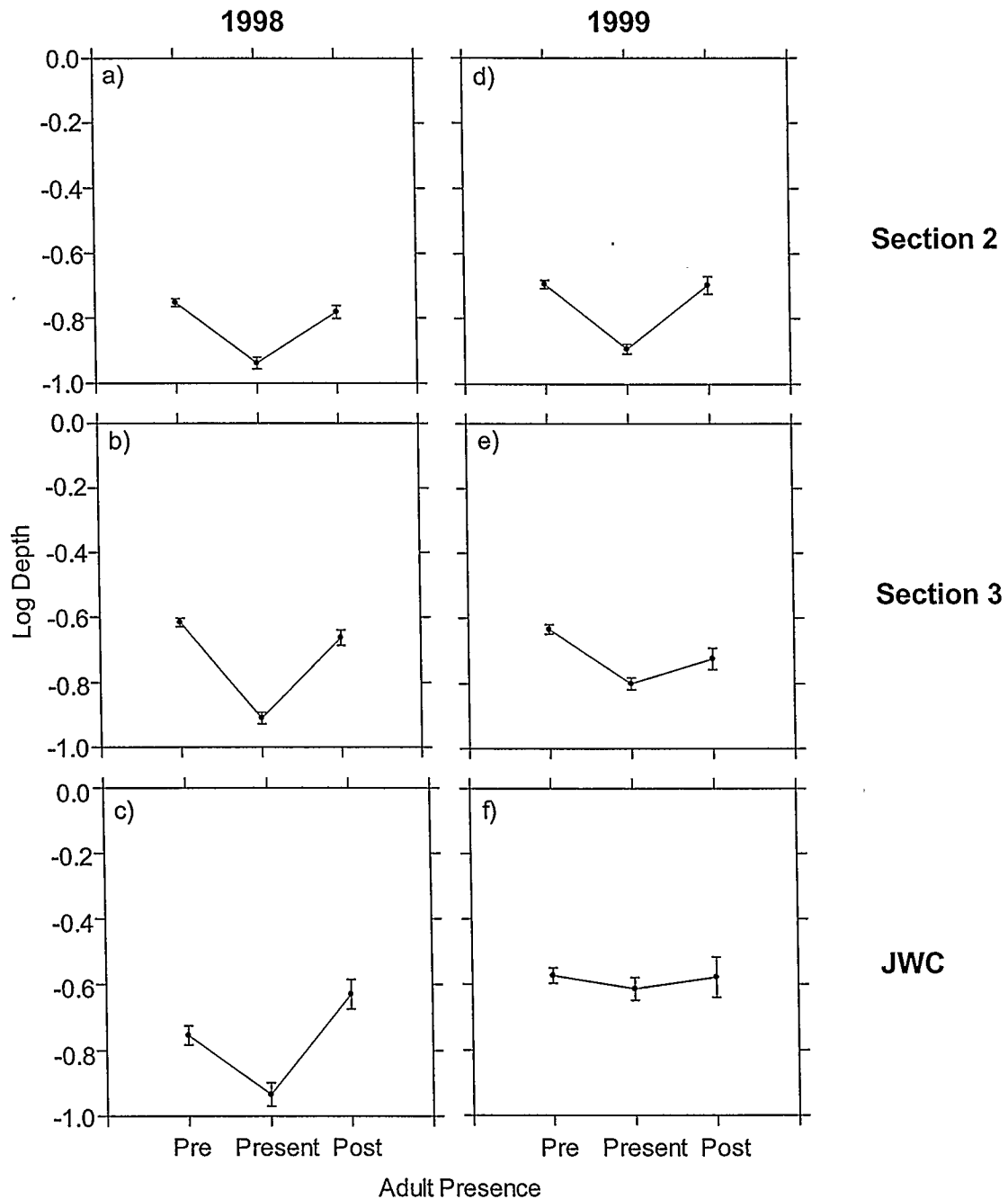


Figure 4.3 ANCOVA results comparing juvenile habitat depth (Log Depth) use in Smith-Dorrien Creek to the presence or absence of adults within the stream in Section 2 (a and d), Section 3 (b and e) and JWC (c and f) for both 1998 (a to c) and 1999 (d to f). To eliminate any effects that size may have on depth use, fork length was included as a covariate. In sections 2 and 3 in both years and JWC in 1998, log depth use was significantly lower when adults were present in the creek compared to both pre- and post-adults. Log depth use was not different between time periods in JWC in 1999. Error bars are standard error (SE)

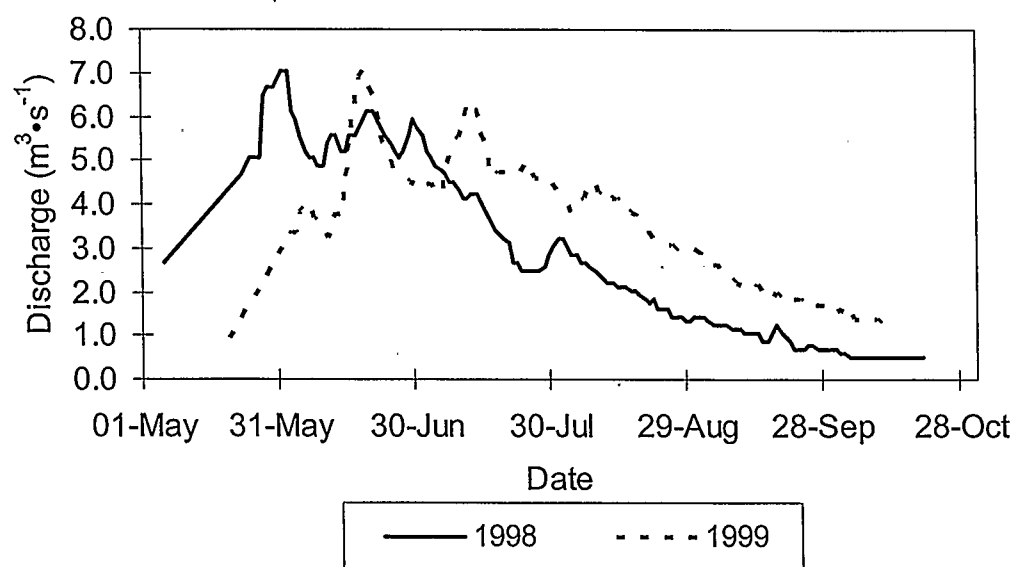


Figure 4.4 Daily discharge measurements ( $\text{m}^3 \cdot \text{s}^{-1}$ ) at the mouth of Smith-Dorrien Creek in 1998 and 1999.



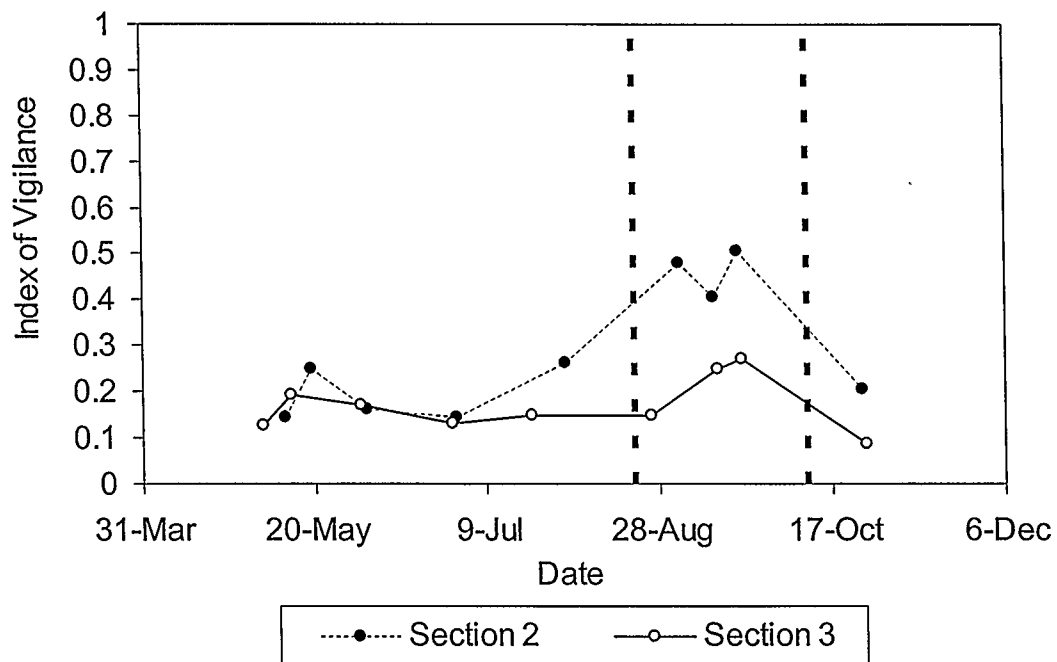


Figure 4.5 Index of vigilance of juvenile bull trout in Smith-Dorrien Creek in both Section 2 and 3 in 1999. The index of vigilance is an effort to quantitatively assess the level of awareness that a juvenile bull trout has of its surroundings (within 0.2 m). The index is calculated as one minus the capture efficiency (proportion of fish successfully caught on first attempt). The time period between the vertical dashed lines indicates when adults had entered the creek.

## Chapter 5 - Summary

This thesis addresses the movements of juvenile (and adult) bull trout within Smith-Dorrien Creek over various scales. The thesis was divided into chapters that investigated various aspects of the movement of juvenile bull trout at various spatial (local within metres, reach-based, stream-based) and temporal scales (diel, daily, weekly, seasonally), and also at different times in the life history (juvenile rearing, ontogenetic shift/migration to adult habitat). Although this thesis focuses on movement and habitat use of juveniles, a large part of Chapter 2 deals with determining environmental variables that may affect the upstream migration of adult bull trout. Little information was available for determining environmental variables that may affect the downstream migration of juveniles. The close association in timing of migration of adults and juveniles suggests that both life stages may respond to similar temperature and flow conditions although for different reasons. The correlation between adult and juvenile movement also hints at the possibility of intraspecific interactions which could affect migration, habitat use, instream movement and survival of juvenile bull trout.

Moving upstream from the confluence of Smith-Dorrien Creek with Lower Kananaskis Lake in Chapter 2, Chapter 3 investigated the diel, daily and seasonal movements and habitat use of juvenile bull trout within the stream. Juvenile bull trout can be divided into two behavioural categories: sedentary and mobile. Sedentary fish account for at least one third of the population and exhibit restricted movement behaviours that coincide with findings of supporters of the restricted movement paradigm. The remaining two thirds are classified as mobile fish, but restrictions in

sampling methods affect confidence in this estimation which is likely high. The range over which sedentary bull trout can move while still maintaining a low displacement was high (up to 200 m), and mainly involved nighttime feeding forays. Daytime refuges were often limited in number and individuals showed fidelity towards particular “home” stones, that were usually composed of cobble/boulder substrate located in pool and run habitat.

Chapter 4 brings aspects of the first two chapters together and examines the effect of adult spawners in the stream on the habitat use and behaviour of juvenile bull trout. There was a significant difference in the depth of habitat used by juvenile bull trout before, during and after adult presence in the stream. Juveniles of all sizes used much shallower habitat while adults were present in the system, minimizing predation risk while still allowing them to be out of cover to feed at night. Unless aggressive behaviour and territory size are reduced during this period, some juveniles are likely to be forced into deeper water where predation risk is high, or to migrate downstream, also increasing the risk of costly interactions with adult conspecifics. Not only did juveniles alter their habitat use, but behaviour was also affected. Juvenile bull trout were found to be increasingly more vigilant during the time period when adults were present in the system. Such behaviour is important in order to assess risks in the environment, but may also affect the ability of fish to feed efficiently.

In a system with a recovering bull trout population, the limiting factor on population density may be juvenile rearing habitat in Smith-Dorrien Creek. My findings suggest that availability of daytime refuge habitat and protective shallow stream habitat may be key

limiting factors creating a negative feedback loop in response to the increasing interaction of adults and juveniles during spawning season.

### Bibliography

- Anderson, W. G., McKinley, R. S. and Colavecchia, M. 1997. The use of clove oil as an anesthetic for rainbow trout and its effects on swimming performance. *North American Journal of Fisheries Management* 17: 301-307
- Anholt, B. R. and Werner, E. E. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology*. 76:2230-2234.
- Bachman, R. A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society*. 113:1-32.
- Baxter, J. S. and McPhail, J. D. 1997. Diel microhabitat preferences of juvenile bull trout in an artificial stream channel. *North American Journal of Fisheries Management*. 17:975-980.
- Beckman, B. R., Larsen, D. A., Lee-Pawlak, B., and Dickhoff, W. W. 1998. Relation of fish size and growth rate to migration of Spring Chinook Salmon smolts. *North American Journal of Fisheries Management*. 18:537-546.
- Begon, M., Harper, J. L, and Townsend, C. R. 1990. *Ecology: individuals, populations and communities*. 2nd Ed. ed. Boston: Blackwell Scientific Publications pp. 160-165.
- Berry, D. K. 1997. Alberta's bull trout management and recovery plan. Mackay, W. C., Brewin, M. K., and Monita, M., eds. *Friends of the bull trout conference proceedings: Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary: Pages 89-98.*
- Bohlin, T., Dellefors, C., and Faremo, U. 1993. Optimal time and size for smolt migration in wild sea trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*. 50:224-232.
- . 1996. Date of smolt migration depends on body-size but not age in wild sea-run brown trout. *Journal of Fish Biology*. 49:157-164.
- Bonneau, J. L. and Scarnecchia, D. L. 1996. Distribution of juvenile bull trout in a thermal gradient of a plunge pool in Granite Creek, Idaho. *Transactions of the American Fisheries Society*. 125:628-630.
- . 1998. Seasonal and diel changes in habitat use by juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in a mountain stream. *Canadian Journal of Zoology*. 76:783-790.

- Bradford, M. J. and Higgins, P. S. 2001. Habitat-, season-, and size-specific variation in diel activity of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Canada Journal of Fisheries and Aquatic Sciences*. 58:365-374.
- Bunnell, D. B. Jr., Isley, J. J., Burrell, K. H., and Van Lear, D. H. 1998. Diel movement of Brown Trout in a Southern Appalachian river. *Transactions of the American Fisheries Society*. 127:630-636.
- Campbell, R. F. and Neuner, J. H. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade Mountain streams. Olson, F. W., White, R. G., and Hamre, R. H. Symposium on Small Hydropower and Fisheries Bethesda, Md.: American Fisheries Society.
- Campbell, R. R. 1990. Rare and endangered fishes and marine mammals of Canada: COSEWIC fish and marine mammals subcommittee status reports: VI. *Canadian Field Naturalist*. 104:1-6.
- Cavender, T. M. 1978. Taxonomy and distribution of the bull trout, (*Salvelinus confluentus*) (Suckley) from the American Northwest. *California Fish and Game*. 64:139-174.
- Chapman, D. W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Research Board of Canada*. 19:1047-1080.
- . 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist*. 100:345-357.
- Erkert, H. G. 1982. Ecological aspects of bat activity rhythms. T.H. Kunz, ed. *Ecology of Bats*. New York: Plenum Press.
- Fraley, J. J. and Shepard, B. B. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead lake and river system, Montana. *Northwest Science*. 63:133-143.
- Fraser, N. H. C, Heggenes, J., Metcalfe, N. B., and Thorpe, J. E. 1995. Low summer temperatures cause juvenile fish to become nocturnal. *Canadian Journal of Zoology*. 73:446-451.
- Fraser, N. H. C. and Metcalfe, N. B. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology*. 11:385-391.
- Gerking, S. D. 1959. The restricted movement of fish populations. *Biological Review of the Cambridge Philosophical Society*. 34:221-242.

- Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*. 68:1856-1862.
- Goetz, F. A. 1989. Biology of the bull trout (*Salvelinus confluentus*) a literature review. Eugene, Oregon: Willamette National Forest.
- a 1997. Diel behaviour of juvenile bull trout and its influence on selection of appropriate sampling techniques. Mackay, W. C., Brewin, M. K., and Monita, M., eds. Friends of the bull trout conference proceedings: Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary: Pages 387-402.
- b 1997. Habitat use of juvenile bull trout in Cascade mountain streams of Oregon and Washington. Mackay, W. C., Brewin, M. K., and Monita, M., eds. Friends of the bull trout conference proceedings: Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary: Pages 339-352.
- Gowan, C. and Fausch, K. D. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences*. 53:1370-1381.
- Gowan, C., Young, M. K., Fausch, K. D., and Riley, S. C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*. 51:2626-2637.
- Grant, J. W. A. 1990. Aggressiveness and the foraging behaviour of young-of-the-year brook charr (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*. 47:915-920.
- Grant, J. W. A. and Kramer, D. L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 47:1724-1737.
- Hansen, L. P. and Jonsson, B. 1985. Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar*) in the River Imsa, Norway. *Aquaculture*. 45:237-248.
- Hartman, G. F. 1965. The role of behaviour in the ecology and interaction of under-yearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*). *Journal of the Fisheries Research Board of Canada*. 22:835-886.
- Harwood, A. J., Metcalfe, N. B., Griffiths, S. W., and Armstrong, J. C. 2002. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*. 59:1515-1523.
- Heggenes, J., Northcote, T. G., and Peter, A. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*. 48:757-762.

- Hilborn, R. and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton, New Jersey: Princeton University Press.
- Hilderbrand, R. H. and Kershner, J. L. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. Transactions of the American Fisheries Society. 129:1160-1170.
- Hillman, T. W., Mullan, J. W., and Griffith, J. S. 1992. Accuracy of underwater counts of juvenile chinook salmon, coho salmon and steelhead. North American Journal of Fisheries Management. 12:598-603.
- Jakober, M. J., McMahon, T. E., Thurow, R. F., and Clancy, C. G. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society. 127:223-235.
- Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research. 66:20-35.
- Kahler, T. H., Roni, P., and Quinn, T. P. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences. 58:1947-1956.
- Krebs, J. R. 1978. Optimal foraging: decision rules for predators. J. Krebs and N.B. Davies. Behavioural Ecology. Oxford: Blackwell Scientific, pp. 23-63.
- Landry, F., Post, J. R., and Parkinson, E. A. 1999. Spatial ontogeny of lentic age-0 rainbow trout, *Oncorhynchus mykiss*: whole lake manipulations of population size structure. Canadian Journal of Fisheries and Aquatic Sciences. 56:1916-1928.
- McCart, P. 1997. Bull trout in Alberta: a review. Mackay, W. C., Brewin, M. K., and Monita, M., eds. Friends of the bull trout conference proceedings: Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary: Pages 191-208.
- McPhail, J. D. and Murray, C. B. 1979. The early life-history and ecology of Dolly Varden (*Salvelinus malma*) in the Upper Arrow Lakes. Prepared for B.C Hydro and Power Authority and Kootenay Region Fish and Wildlife:113 pp.
- Metcalf, N. B., Fraser, N. H. C., and Burns, M. D. 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. Proceedings of the Royal Society of London Series B, Biological Science. 265:1503-1507
- .1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology. 68:371-381.



- Miller, R. B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. *Journal of the Fisheries Research Board of Canada*. 14:687-691.
- Miller, T. J., Crowder, L. B., Rice, J. A., and Marschall, E. A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*. 45:1657-1670.
- Mittelbach, G. G. 1986. Predator-mediated habitat use: some consequences for species interactions. *Environmental Biology of Fishes*. 16:159-169.
- Mushens, C. J., Johnston, F. D., and Post, J. R. 2003. Population dynamics of the Lower Kananaskis Lake bull trout: 1995-2000 Final Report. Calgary, AB.: University of Calgary Prepared for the Alberta Conservation Association and TransAlta Utilities. 71 pp. + app.
- Naesje, T. F., Jonsson, B., and Sandlund, O. T. 1986. Drift of cisco and whitefish larvae in a Norwegian River. *Transactions of the American Fisheries Society*. 115:89-93.
- Nakano, S., Fausch, K. D., Furukawa-Tanaka, T., Maekawa, K., and Kawanabe, H. 1992. Resource utilization in bull char and cutthroat trout in a mountain stream in Montana, U.S.A. *Japanese Journal of Ichthyology*. 39:211-216.
- Nakano, S., Kitano, S., Nakai, K., and Fausch, K. D. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environmental Biology of Fishes*. 52:345-355.
- Nielson, L. A. and Johnson, O. L. 1983. *Fisheries Techniques*. Bethesda, Maryland, USA. 468 pp.: AFS publications.
- Northcote, T.G. 1984. Mechanisms of fish migration in rivers. Mechanisms of migration in fishes. McCleave, J. D., Arnold, G. P., Dodson, J. J., Neill, W. H., eds. New York: Plenum Press.
- . 1992. Migration and residency in stream salmonids - some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Research*. 67:5-17.
- . 1997. Potamodromy in salmonidae - living and moving in the fast lane. *North American Journal of Fisheries Management*. 17:1029-1045.
- Paul, A. J. 2000. Recruitment dynamics in bull trout (*Salvelinus confluentus*): Linking theory and data to species management. Ph.D. thesis: University of Calgary, Calgary, AB.
- Post, J. R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. *Canadian Journal of Fisheries and Aquatic Sciences*. 47(3):554-560.

- Post, J. R. and Johnston, F. D. 2001. The status of bull trout (*Salvelinus confluentus*) in Alberta. Edmonton, AB.: Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association Status Report No. 39.
- Post, J. R., Parkinson, E. A., and Johnston, N. T. 1998. Spatial and temporal variation in risk to piscivory of age-0 rainbow trout: patterns and population consequences. *Transactions of the American Fisheries Society*. 127:932-942.
- . 1999. Density-dependent processes in structured fish populations: assessment of interaction strengths in whole-lake experiments. *Ecological Monographs*. 69:155-175.
- Prentice, E. F., Flagg, T. A., and McCutcheon, C. S. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium*. 7:317-322.
- Quinn, T. P., Hodgson, S., and Peven, C. 1997. Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia river. *Canadian Journal of Fisheries and Aquatic Sciences*. 54:1349-1360.
- Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*. 54:1211-1234.
- Riehle, M. D. and Griffith, J. S. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter. *Canadian Journal of Fisheries and Aquatic Sciences*. 50:2119-2128.
- Riehle, M., Weber, W., Stuart, A. M., Thiesfeld, S. L., and Ratliff, D. E. 1997. Progress report of the multi-agency study of bull trout in the Metolius River system, Oregon. Mackay, W. C., Brewin, M. K., and Monita, M., eds. *Friends of the bull trout conference proceedings: Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary: Pages 137-146.*
- Rieman, B. E. and McIntyre, J. D. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society*. 124:285-296.
- Riley, S. C. and Fausch, K. D. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. *North American Journal of Fisheries Management*. 12:768-776.
- Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology*. 83:1-13.

- Rosenfeld, J. S. and Boss, S. B. 2001. Fitness consequences of habitat use of juvenile cutthroat trout: energetic costs and benefits in pools and riffles. *Canadian Journal of Fisheries and Aquatic Sciences*. 58:585-593.
- Saffel, P. D. and Scarnecchia, D. L. 1995. Habitat use by juvenile bull trout in Belt-series geology watersheds of northern Idaho. *Northwest Science*. 69:304-317.
- Salonen, K., Jones, R. I., and Arvola, L. 1984. Hypolimnetic retrieval by diel vertical migrations of lake phytoplankton. *Freshwater Biology*. 14:431-438.
- Shepard, B. B., Pratt, K. L., and Graham, P. J. 1984. Life histories of Westslope cutthroat and bull trout in the Upper Flathead River basin, Montana. Environmental Protection Agency, Region VIII, Water Division, Denver Colorado R008224-01-5.
- Shuter, B. J. and Post, J. R. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society*. 119:314-336.
- Slaney, P. A. and Northcote, T. G. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *Journal of the Fisheries Research Board of Canada*. 31:1201-1209.
- Smithson, E. B and Johnston, C. E. 1999. Movement patterns of stream fishes in a Ouachita Highlands stream: and examination of the restricted movement paradigm. *Transactions of the American Fisheries Society*. 128:847-853.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*. 3rd. ed. New York: W.H. Freeman and Company.
- Solomon, D. J. 1978. Some observations on salmon smolt migrations in a chalkstream. *Journal of Fish Biology*. 12:571-574.
- Stelfox, J. D. 1997. Seasonal movements, growth, survival and population status of the adfluvial bull trout population in lower Kananaskis Lake, Alberta. Mackay, W. C., Brewin, M. K., and Monita, M., eds. *Friends of the bull trout conference proceedings: Bull Trout Task Force (Alberta)*, c/o Trout Unlimited Canada, Calgary: Pages 309-316.
- Swanberg, T. R. 1997. Movements of and habitat use by fluvial Bull Trout in the Blackfoot River, Montana. *Transactions of the American Fisheries Society*. 126:735-746.
- Tabor, R. A. and Wurtsbaugh, W. A. 1991. Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. *Transactions of the American Fisheries Society*. 120:728-738.

- Thorpe, J. E. 1987. Smolting versus residency: Developmental conflict in salmonids. American Fisheries Society Symposium. 1:244-252.
- Thurrow, R. F. 1997. Habitat utilization and diel behaviour of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fishes. 6:1-7.
- Watson, G. and Hillman, T. W. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. North American Journal of Fisheries Management. 17:237-252.
- Webb, P. W. 1978. Temperature effects on acceleration of rainbow trout, (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada. 35:1417-1422.
- Werner, E. E. and Anholt, B. R. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. The American Naturalist. 142:242-272.
- Werner, E. E. and Gilliam, J. F. 1984. The ontogenetic niche shift and species interactions in size-structured populations. Annual Review of Ecology and Systematics. 15:393-425.
- Werner, E. E., Gilliam, J. F., Hall, D. J., and Mittelbach, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology. 64:1540-1548.
- Werner, E. E. and Hall, D. J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology. 69:1352-1366.
- Werner, E. E., Mittelbach, G. G., Hall, D. J., and Gilliam, J. F. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology. 64:1525-1539.
- Wilkinson, L., Hill, M., Welna, J. P., and Birkenbeuel, G. K. 1992. Systat for windows: Statistics, Version 5 edition. SYSTAT, Inc., IL.
- Young, M. K. 1998. Absence of autumnal changes in habitat use and location of adult Colorado River Cutthroat Trout in a small stream. Transactions of the American Fisheries Society. 127:147-151.
- . 1994. Mobility of brown trout in south-central Wyoming streams. Canadian Journal of Zoology. 72:2078-2083.