Adult distribution and the effects of dispersal and genetic drift on population genetic structure of resident rainbow trout (Oncorhynchus mykiss) in Babine Lake, British Columbia.

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ADULT DISTRIBUTION AND THE EFFECTS OF DISPERAL AND GENETIC DRIFT ON POPULATION GENETIC STRUCTURE OF RESIDENT RAINBOW TROUT (Oncorhynchus mykiss) IN BABINE LAKE, BRITISH COLUMBIA

By

Rachel Anne Koehler

A Thesis
Submitted to the Faculty of Graduate Studies and Research through Environmental Science in Partial Fulfillment of the Requirements for the Degree of Master of Science at the University of Windsor

Windsor, Ontario, Canada

2010

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ABSTRACT

Resident rainbow trout in Babine Lake, British Columbia are the focus of regionally important recreational and First Nations food fisheries. This study investigates the roles of dispersal and random genetic drift on lake-wide population genetic structure and non-random distribution of adults. Using thirteen microsatellite loci, I found strong divergence between tributary populations and parr and fry life-stages within tributaries. I found that juvenile dispersal did not greatly affect the divergence between parr and fry groups, but that random genetic drift due to low effective population size was the likely cause of divergence between parr and fry. Adult distribution in the lake was non-random and may have been driven by habitat partitioning. This study demonstrates that high genetic divergence between life-stages, random genetic drift, and non-random distribution of fish are critical factors that should be considered when evaluating evolutionary processes and considering management options.
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1.0 General Introduction

Recent trends in conservation and management have focused on overall ecosystem health, maintenance of biodiversity, and the fitness and viability of populations (Haig 1998). An important component of long-term ecosystem health is the genetic composition and diversity of populations within the ecosystem. Maintenance of genetic health and diversity is important to the continued persistence of populations (Frankham 2003). Loss of genetic diversity can severely limit the ability of a population to cope with changes in the environment and adapt to new conditions (Reed & Frankham 2003). Development of a metapopulation structure characterized by high levels of local extinction and recolonization (Frankham et al. 2002) can have many negative implications for conservation, such as low effective population sizes and greater loss of genetic diversity (Wang & Caballero 1999). Decreased population sizes may lead to inbreeding which can result in lower reproductive fitness and exposure of recessive deleterious alleles (Frankham et al. 2002). In salmonid populations that are comprised of several unique reproductive assemblages, the loss of a single reproductive assemblage can mean the loss of a large amount of unique genetic diversity, therefore the continued persistence of reproductive assemblages may be critical for the entire population in a system.

Although individuals within a species can interbreed with one another, panmixia throughout their distribution is unlikely. Instead, there are generally many populations, or stocks, that make up a species. In the case of an exploited resource, such as a fishery,
understanding the contribution of each stock to the fishery is important for management and conservation. Knowing the proportion of fish contributed by each stock to a fishery can allow managers to set regulations that avoid overharvesting individual stocks and protect weaker stocks. For genetic analyses, stocks must have sufficient genetic differentiation between one another for identification and estimation of relative contribution to the fishery (Utter & Ryman 1993).

Species are not uniform, but rather they often display behavioral, morphological, or genetic differences over the extent of their distribution (Taylor 1991, Frankham 2003, Allendorf & Luikart 2007, Lowe et al. 2005). These differences can be the result of local adaptation, a process which results in populations that are genetically different from one another and have higher frequencies of traits that enhance survival in a particular location (Taylor 1991). Local adaptation has profound implications for conservation and management efforts because locally adapted populations may store valuable genetic diversity critical for long-term viability (Dodson et al. 1998).

Populations must have sufficient levels of reproductive isolation for local adaptation to occur (Aspinwall 1974). Reproductive isolation can occur both pre- and postzygotically. Postzygotic isolation can occur as hybrid sterility or inviability and can be influenced by the environment. Prezygotic isolation occurs when mating between individuals is not possible or fertilization is not successful due to some incompatibility. Reinforcement
also plays a role in reproductive isolation when natural selection increases prezygotic isolation between sympatric populations or species (Coyne & Orr 2004). Measuring reproductive isolation can be difficult, but the use of neutral genetic markers has made it possible to estimate levels of gene flow and dispersal, even in systems where it is difficult or impossible to track individual dispersal and reproduction (Slatkin & Barton 1989, Gaggiotti et al. 1999). Organisms may disperse to other populations, but unless those migrants successfully reproduce and contribute genetic material to the population, they are not contributing to gene flow. Thus there is an important difference between dispersal and gene flow; however, gene flow is not possible without dispersal at some life stage. Limited gene flow creates a greater opportunity for genetic divergence driven either by random genetic drift or selection (Frankham et al. 2002). This in turn may lead to the development of local adaptation and eventually speciation (Lowe et al. 2005). However, there is some evidence indicating that speciation can occur with gene flow (Nosil 2008).

Genetic drift is one of the evolutionary forces impacting small populations, but it also affects populations with large census sizes. Effective population size ($N_e$) is an estimate of the size of an ideal population that is losing genetic diversity at the same rate as observed in a population. Fluctuations in population size over time, unequal sex ratios, and variance in reproductive success all influence $N_e$ (Conner & Hartl 2004). Consequently, the rate of loss of genetic diversity is determined not by census size, but
by $N_e$ (Kalinowski & Waples 2002). Very low estimates of $N_e$ can result in rapid genetic divergence by drift and may increase the risk of extinction (Newman & Pilson 1997).

Rainbow trout (RBT, *Oncorhynchus mykiss*) exist as both anadromous and resident forms. Anadromous fish are known as steelhead and spend a portion of their life at sea where they can attain large body sizes. Resident fish are referred to as rainbow trout and spend their entire lives in fresh water; however they often display migratory behavior within fresh water. The native range of RBT extends from the Kuskokwim River, Alaska to northwest Mexico in North America and on the Kamchatka Peninsula in Russia (Quinn 2005). In general, RBT prefer cool, well-oxygenated waters. RBT are opportunistic feeders and eat aquatic insects, terrestrial insects, zooplankton, fish eggs, algae, and fish. Adult RBT may attain sizes of 2-5kg (Wydoski & Whitney 1979).

RBT spawn in tributaries of lakes or rivers in the spring and juvenile RBT emerge as fry later in the summer (Wydoski & Whitney 1979) and remain in the tributaries. After the first year juveniles are known as parr and continue to rear in the tributaries, typically for two or more years before moving into a lake or river. Unlike other Pacific salmonids, RBT are iteroparous (Quinn 2005) and can spawn year after year. Sub-adult and adult resident RBT remain in the lake most of the year and return to tributaries to spawn. RBT display natal philopatry and return to their natal stream to reproduce (Quinn 2005). Because of their homing behavior, RBT populations have been found to have population
structure at the regional and within-drainage level (Krueger et al. 1999, Narum et al. 2006). There is great opportunity for local adaptation and divergence among populations, because RBT populations are generally not subject to high levels of extinction and recolonization.

Babine Lake in northwestern British Columbia has populations of both anadromous and resident RBT. The resident RBT reside in the lake as adults and spawn in its many tributaries. The longest unimpounded natural lake in BC, Babine Lake is approximately 177 km in length. Babine Lake supports the largest recreational RBT fishery in Skeena Region, with over 18,000 angler days in 2005 (Gislason 2009). Due to its location in traditional First Nations land, Babine Lake also supports a First Nations food fishery. Therefore, Babine Lake RBT fishery is both economically and socially important to the region. Babine Lake is fed by many tributaries, and it is estimated that 88% of RBT production in the lake occurs in eight of the tributaries (Bustard 1989). The outflow of the lake is the Babine River which is located at the northern end of the lake. This section of river adjacent to the lake is known as Rainbow Alley and connects Babine Lake to the nearby Nilkitkwa Lake. Both Rainbow Alley and Nilkitkwa Lake support popular recreational RBT fisheries. Babine Lake also supports a large sockeye salmon (Oncorhynchus nerka) population (Bustard 1989) and juvenile sockeye and kokanee are a food source for rainbow trout as well as Lake char (S. namaycush).
1.1 Thesis objective

The overall goal of this study was to determine the lake-level population genetic structure and adult distribution patterns in resident rainbow trout using the Babine Lake RBT population as a model system.

1.2 Chapter 2 objective

Within a species, populations may display morphological, behavioral, or genetic differences across their range (Taylor 1991, Frankham et al. 2002, Allendorf & Luikart 2007, Lowe et al. 2005), which may be due to local adaptation. If selection pressures vary among locations, and there is reproductive isolation or limited gene flow between populations, those populations may adapt to their environment to become better suited to a particular area. With reproductive isolation and limited gene flow there is greater opportunity for genetic divergence either by drift or selection (Frankham et al. 2002), and consequently for the development of local adaptation.

The purpose of this portion of the study was to examine the population genetic structure of a lake-level system and to investigate the roles of life-stage specific dispersal and random genetic drift in the development of population structure to provide a better understanding of evolutionary processes.
Patterns of dispersal and distribution in fish can be complex and variable over the course of their life. Factors such as differential dispersal ability, relatedness (Griffiths et al. 2003, Quinn & Busack 1985), and habitat partitioning (George & Hadley 1979, Matthews & Hill 1980, Ross 1986) may drive some patterns of distribution. Babine Lake resident RBT are an important resource in Skeena Region, but the distribution patterns of adults from various tributary stocks are unknown.

The purpose of this portion of the study was to use genotype assignment to identify the source tributaries for adult RBT caught throughout Babine Lake and characterize the dispersal patterns of resident RBT in Babine Lake to improve the management of this valuable species.
1.4 References


2.0 Life stage specific dispersal and genetic drift effects on spatial genetic structure in Babine Lake tributary rainbow trout

2.1 Introduction

Within a species, populations often display morphological, behavioral, or genetic differences across their range (Taylor 1991, Frankham 2002, Allendorf & Luikart 2007, Lowe et al. 2005). These differences can be the result of local adaptation, a process which results in populations that are genetically different from one another and have higher frequencies of traits that enhance survival in a particular location (Taylor 1991). If there is limited gene flow between populations and selection pressures vary among locations, those populations may adapt to their environment to become better suited to a particular area. For example, sculpins in Alaska may match the coloration of river substrates (which varies across the landscape), presumably to reduce predation risk (Whitely et al. 2009). Similarly, Alaskan sockeye salmon egg size is highly correlated with the size of the substrate onto which eggs were deposited, again presumably to maximize egg survival (Quinn et al. 1995). Since local adaptation can also affect reproductive cues or mate preferences (Servedio 2004), reproductive isolation or gene flow may be reinforced and local adaptation can lead to speciation over time (Lowe et al. 2005). The presence or absence of local adaptation has substantial implications for conservation and management since locally adapted populations represent evolutionarily significant units (ESUs) which may harbor valuable genetic variation critical for long-term viability (Dodson et al. 1998).
However, along with different selective pressures, there must be a restriction in gene flow between populations for local adaptation to occur (Aspinwall 1974). With limited gene flow there is greater opportunity for genetic divergence either by drift or selection (Frankham et al. 2002), and hence for the development of local adaptation. Although measuring reproductive isolation directly can be logistically difficult, neutral genetic markers can be used to estimate levels of gene flow and dispersal (Slatkin & Barton 1989, Gaggiotti et al. 1999). Larval or juvenile fish may move to other populations, but unless those individuals contribute genetically to the population there is no gene flow. Many factors influence gene flow among populations, for instance distance between populations (e.g. Salvelinus fontinalis, Salmo salar, Salvelinus alpinus in Gomez-Uchida et al. 2009), natural barriers such as waterfalls (e.g. Poecilia reticulata in Crispo et al. 2006), man-made barriers such as dams (e.g. O. mykiss in Deiner et al. 2007) or culverts (e.g. O. clarkii in Wofford et al. 2005), and temporally staggered spawning times (e.g. O. tshawytscha in Banks et al. 2000). The characterization of gene flow is further complicated by life-stage specific dispersal. For example, in salmonids, adults disperse over large areas, while juveniles remain relatively sedentary or disperse to a lesser extent. Estimation of dispersal and gene flow, and the characterization of the factors that control it, is critical for conservation and for our understanding of evolution because of the substantial impacts it can have on local adaptation potential, especially in heterogeneous environments where local adaptation is expected to occur (Slatkin 1987, Galloway & Fenster 2000).
Random changes in allele frequencies, or genetic drift, may also play a role in population genetic divergence. In small populations, genetic drift will result in random genetic changes from generation to generation and can lead to a loss of genetic diversity and the fixation of alleles (possibly deleterious) within a population (Frankham et al. 2002). Unlike genetic changes due to selection, genetic drift does not specifically drive a population towards a beneficial adaptation or away from a deleterious phenotype. Larger populations often have greater genetic diversity which allows them to be more responsive to selective forces, whereas small populations are more subject to random genetic changes and often have less genetic diversity (Frankham et al. 2002).

Genetic drift is commonly identified as an evolutionary force in small populations, but it may also play an important role in populations that appear large. Effective population size ($N_e$) is the size of an ideal population that would be affected by genetic drift at the same rate as the actual population. And it is $N_e$ rather than census size that determines the rate of loss of genetic diversity (Kalinowski & Waples 2002). Heath et al. (2002) found that $N_e$ was much smaller than the population census size ($N$) in several populations of steelhead trout, and in general, the $N_e:N$ ratio is generally very low for salmonid populations (e.g., Shrimpton & Heath 2003). Therefore a moderate to large $N$ does not mean that a population will not be subject to random genetic drift. Small effective population size can play an important role in changes in genetic variability over time (Frankham et al. 2002) and very low estimates of $N_e$ will lead to very fast genetic divergence by drift and may increase the risk of extinction (Newman & Pilson 1997).
The home range of salmonid fishes can be extremely large due to the fact that a portion of their life is spent in freshwater for rearing and reproduction and several years may be spent at sea (Quinn 2005). Salmonids are also known for their impressive displays of natal philopatry, or homing (Dittman & Quinn 1996). Rates of homing can be as high as 98% in some populations (Quinn & Fresh 1984) and this behavior results in complex genetic structuring across the range of a species (Dittman & Quinn 1996). In some cases, homing can also be very precise. Stewart et al. (2003) found that sockeye salmon spawning at different island beaches approximately 5.5 to 14 km apart in Iliamna Lake, Alaska formed genetically distinct populations. Salmonids sometimes display genetic differentiation at microgeographic scales, for example within the tributaries of a lake or within a river (Garant et al. 2000), in geographically close lakes (Angers et al. 1995), or in a river system (Spruell et al. 1999). Although genetic population divergence at a fine-scale is important in the development of local adaptation, genetic structure within lakes has been investigated in relatively few studies. Though homing may be common in salmonids, not all fish return to their natal habitat and the straying fish can contribute to gene flow among populations if they survive and reproduce, thus limiting genetic divergence of populations. Therefore, it is important to determine the levels of dispersal at various life stages, since despite known straying (Quinn & Fresh 1984), salmon populations generally exhibit substantial genetic differentiation.
Rainbow trout (*Oncorhynchus mykiss*) is an excellent study species for examining population genetic differentiation and gene flow at small spatial scales. Like other Pacific salmonids, rainbow trout (RBT) display natal philopatry and return to their tributaries to spawn in the late spring (Quinn 2005). Unlike other Pacific salmon, however, RBT are iteroparous and can return to spawn year after year (Quinn 2005). Structure has been found among RBT populations at both the regional and within-drainage level (Krueger *et al.* 1999, Narum *et al.* 2006). RBT populations are generally not subject to high levels of extinction and recolonization, so there is great opportunity for local adaptation and divergence between populations.

In this study I examine the genetic differences between tributary populations of resident RBT in Babine Lake. Because of the size of the lake and anecdotal information, I suspect that there is genetic structure between tributaries, but it is unknown what factors contribute to those patterns of divergence. It is possible that local adaptation has occurred in the system, which would be a conservation concern, but proving local adaptation is present and implementing a management strategy to address it would be difficult. My hypothesis is that life-stage specific dispersal and genetic drift are affecting lake-wide spatial genetic structure among the nursery tributary habitats. To address this hypothesis, tissue samples were collected from juvenile RBT in tributaries around the lake during two summers to allow both spatial and temporal comparisons of genetic differentiation within a single system. Investigation of the role of life-stage specific
dispersal and genetic drift in the development of spatial genetic structure is an important step to improve management and better understanding of evolutionary processes.

2.2 Materials and Methods

Study System and Species

*Oncorhynchus mykiss* exists in both anadromous and resident forms. Anadromous fish are known as steelhead trout and spend a portion of their life at sea where they can attain large body sizes before they return to their natal stream to spawn. Resident fish are referred to as rainbow trout and spend their entire lives in fresh water. Both forms are iteroparous (Quinn 2005). Babine Lake in northwestern British Columbia (126° 0' 0"/54° 45' 30", Figure 2.1), has resident RBT that reside in the lake as adults and spawn in its tributaries. Juvenile RBT emerge as fry in late July or early August (Bustard 1989). After the first year juveniles are known as parr and rear in the tributaries, typically for two or more years before moving into the lake. In this study, I sampled sub-adult resident RBT in Babine Lake tributaries. Babine Lake is the longest unimpounded natural lake in BC and supports the largest recreational RBT fishery in the region as well as supplying First Nations food fisheries. Because of the large number of stakeholders, the Babine Lake RBT fishery is both economically and socially important to the region. Babine Lake is fed by many tributaries (Figure 2.1), eight of which are suspected of producing 88% of the RBT in the lake (Bustard 1989). The outflow is the Babine River at the northern end of the lake (Figure 2.1).
Figure 2.1 Map of Babine Lake with the location of tributary sampling sites marked. Circles mark sites that were sampled in one year, squares mark sites that were sampled in 2006 and 2008. Lines indicate the division of geographic regions. See Table 2.1 for site names and coordinates.
Sample Collection

To determine the genetic population structure of Babine Lake tributaries, juvenile (fry and parr) RBT were collected from Babine Lake tributaries in 2006 and 2008. To most effectively sample the system, tributaries in which RBT had been detected in previous surveys or were suspected of juvenile RBT production, including the seven of the eight tributaries suspected of producing 88% of juveniles, (Bustard 1989) were targeted. Juvenile fish were collected with minnow traps (baited with salmon roe) and by electrofishing (single pass using a Smith-Root Model 15B generator powered backpack electrofisher and a Model 12B battery powered backpack electrofisher).

In August 2006, 350 juvenile RBT were collected from six Babine Lake tributaries. In August and September 2008 those tributaries were re-sampled and twelve additional tributaries were sampled (Figure 2.1) with a total of 850 juvenile RBT collected. Sample sites were grouped into six broad geographic regions representing basins within the lake: Lower Babine (NKB, NYC, BCC, BFC, DJC, BBR), North (HEA, 11MC, 5MC, TSA), Morrison (UMT), Main (HAG, RRC, WIL, TAC), South (CRC, DNC, GWC), and Sutherland (SRI). All fish were measured for fork length (mm) and a small adipose or caudal fin clip was collected from each fish over 40 mm fork length and stored in 95% ethanol or a high salt buffer for subsequent DNA extraction. Fish less than 40mm in length were humanely sacrificed and stored whole in the same manner. Juvenile fish with a fork length greater than or equal to 60 mm were classified as parr (1+ to 3+ year old) and those less than 60 mm were classified as fry (0+ year old). For some sites, parr
and fry were not differentiated and the sample consisted of fin clip mixtures of the two life stages (Table 2.1).

**Table 2.1** Sample site and genetic summary for juvenile rainbow trout (*O. mykiss*) collected in Babine Lake, British Columbia, tributaries. Sample site name and code, sample year, geographic location, sample size (N), mean heterozygosity (H), and loci out of Hardy Weinberg equilibrium for all sample sites are given.

<table>
<thead>
<tr>
<th>Site†</th>
<th>Code</th>
<th>Year</th>
<th>Site Easting, Northing</th>
<th>N*</th>
<th>Parr</th>
<th>Mean H**</th>
<th>Loci out of HWE</th>
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<td>0.692</td>
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*Numbers in bold signify a mix of parr and fry samples.
**Numbers in bold indicate that parr and fry were combined to calculate mean heterozygosity. This was done when a parr or fry group at a site had fewer than 15 individuals sampled or when parr and fry were not separated.
†The tributaries that produce the most juveniles are bolded.
DNA Extraction and Microsatellite Genotyping

DNA was extracted from 1,200 juvenile RBT samples using the column-based plate extraction method described in Elphinstone et al. (2003). All individuals were genotyped at thirteen microsatellite loci that were previously developed for RBT and other Pacific salmonids: Ots3 and Ots4 (Banks et al. 1999) with 11 and 13 alleles respectively; Ots243, OtsG401, OtsG43, OtsG253b, OtsG249, and OtsG83b (Williamson et al. 2002) with 4, 17, 14, 26, 24, and 25 alleles respectively; RT191, RT212, and RT561 (Spies et al. 2005) with 23, 29, and 9 alleles respectively; Omy325 (Olsen et al. 1996) with 29 alleles; and ONE101 (Olsen et al. 2000) with 13 alleles. Polymerase chain reaction (PCR) conditions were optimized for each locus and each reaction used approximately 50 ng of template DNA, 1.10 μl 10X Buffer, 1.10 μl 25 mM MgCl2, 0.20 μl 40 μM dNTPs, 0.20 μl forward and reverse primers, and 0.15 U of Taq polymerase. All thermocycler protocols began with a 2 minute denaturation cycle at 94.0°C, followed by 35 cycles of denaturation at 94.0°C for 15 s, annealing at a locus specific temperature for 45 s (52.0°C for Ots and Ots243; 55.0°C for Ots4; 56.0°C for OtsG83B and Omy325; 58.0°C for RT212, OtsG253B, and OtsG249; 59.0°C for ONE101; 61.0°C for OtsG43; 62.0°C for OtsG401 and RT561; and 63.0°C for RT191), and extension at 72.0°C for 30 s, and ended with a final 2 minute extension at 72.0°C. PCR product fragment size was determined using a LiCor 4300 DNA analyzer and GeneImagr software (Scanlytics, Inc.).
Genetic Analyses

All 13 microsatellite loci were tested for departures from Hardy-Weinberg equilibrium using 10,000 dememorisation steps, 100 batches, and 5,000 iterations per batch in GenePop v4.06 (Rousset 2007) and significance was adjusted for multiple tests using the Bonferroni method (Rice 1989). To verify that 60 mm was an appropriate length at which to separate parr and fry, a histogram of juvenile fork length across all sampling sites was constructed.

I used only juveniles sampled in 2008 that could be separated into parr and fry to characterize the spatial genetic structure of RBT in Babine Lake tributaries. First, a global $F_{ST}$ across all sample groups (parr and fry separate) was calculated in Tools for Population Genetic Analysis v1.3 (TFPGA, Miller 1997). Next, within each sampled tributary, I compared fry and parr using exact tests of allele frequency distribution divergence with 10,000 permutations (Raymond & Rousset 2005) in Tools for Population Genetic Analysis v1.3 (TFPGA, Miller 1997) and significance was adjusted for multiple tests using the Bonferroni method (Rice 1989). I unexpectedly found consistent and substantial genetic divergence between the parr and fry collected in the same tributary. Thus, to explore the potential causes of the parr-fry divergence, I performed a series of analyses designed to characterize the nature of the genetic divergence between life-stages and its effect on the system: 1) to test for life-stage specific dispersal, I used genotype assignment to identify the dispersing fry and parr in Babine Lake tributaries and to characterize the dispersal path; 2) to test for kin aggregation in the newly hatched fry, I
estimated and compared relatedness in parr and fry at all sampled sites; and 3) to quantify the role of genetic drift in the observed parr-fry divergence, I performed temporal genetic analyses and estimated effective population sizes of the parr vs fry.

1) Life-stage specific dispersal: I used genotype assignment to identify the likely source of the parr through assignment to fry source populations using GeneClass 2.0.h (Piry et al. 2004). Parr were assigned to fry source populations because parr are more likely to disperse than the smaller, younger fry. A two-step process was used to perform the assignment. First, a probability computation utilizing Monte-Carlo resampling (Paetkau et al. 2004) was used to exclude parr that likely originated from an un-sampled population or tributary. If a parr had a less than 10% probability of being assigned to any sampled fry source population, then that fish was excluded from further assignment. Next, the remaining parr were assigned to fry sample groups using a rank-based method (Rannala & Mountain 1997). The five most likely fry source populations were ranked. The majority of fish (57.0%) had a 9 times or greater difference between the first and second ranked tributaries; however, to determine the sensitivity of my analysis to my choice of assignment threshold, I performed a sensitivity analysis where I varied the assignment probability threshold and evaluated the effect on the number of fish successfully assigned (Figure 2.2). Because designating a threshold value in the range of 3x to 9x would not greatly change the number of assigned individuals, the value of 4x was selected as it has been used successfully in other studies (e.g., Beneteau et al. 2009).
If the difference was less than four times, the fish was not assigned to any fry sample group and deemed “unassigned”.

![Bar graph](image)

**Figure 2.2** Sensitivity analysis of number of Babine Lake, BC rainbow trout (*O. mykiss*) parr assigned to a fry source when various ratios of the probability of assigning to the first ranked fry source vs the second ranked fry source are used. The open bar indicates the total number of parr.

To test my assumption that fry were unlikely to stray, I used genotype assignment in GeneClass 2.0.h (Piry et al. 2004) to determine the number of fry in each tributary that are likely strays from another tributary population. The two-step assignment process using a 4x threshold value as described above was used to assign fry to fry source populations (“leave one out” procedure). It was important to determine if the fry in the source populations self-assign because detection of dispersed parr through genotype assignment relies on accurate fry source populations.
Once I identified dispersing parr based on genotype assignment, I estimated the effect of the strays on population genetic structure by removing the stray parr from the tributary sample groups and comparing genetic structure before and after the removal of dispersing fish. The expectation was that removal of dispersing parr would increase genetic divergence between tributaries and decrease the amount of genetic variation in the system resulting from genetic differences between life-stages (and hence decrease the genetic divergence between parr and fry groups). A global $F_{ST}$ for all parr sample groups was calculated in Tools for Population Genetic Analysis v1.3 (Miller 1997) before and after removal of dispersed parr. Pairwise $F_{ST}$ between parr and fry groups within individual tributaries, as well as between parr groups among tributaries was calculated in Arlequin v3.11 (Excoffier et al. 2005) before and after removal of dispersed parr. Parr vs fry pairwise $F_{ST}$ before and after removal of strays was plotted to investigate the role of dispersed parr on genetic divergence between life-stages. Parr vs parr pairwise $F_{ST}$ before and after removal of strays was plotted to examine the role of dispersed parr on spatial structure. T-tests were performed in Systat (v7.0.1) to determine if the change in $F_{ST}$ before and after removal of dispersed parr (i.e. $\Delta F_{ST} = (F_{ST(\text{before})} - F_{ST(\text{after})})$) was different from zero.

Next, a nested hierarchical analysis of molecular variance (AMOVA) with 10000 permutations (Arlequin v3.11, Excoffier et al. 2005) was performed among life-stage groups (parr and fry collected in 2008) nested within sample site (11MC, BCC, CRC, DNC, GWC, RRC, SRI, UMT, WIL) before and after the removal of dispersed parr to
partition the genetic variance among age groups within sample sites at the lake-wide level. To test for an isolation by distance model of genetic structure, pairwise $F_{ST}/(1-F_{ST})$ (Slatkin 1995) was calculated in Arlequin v3.11 (Excoffier et al. 2005) for fry groups, parr groups before removal of dispersed parr, and parr after removal of dispersed parr. $F_{ST}/(1-F_{ST})$ was used because it is more easily interpreted in situations where habitat is long and narrow (Rousset 1997). The $F_{ST}/(1-F_{ST})$ values were plotted against the pairwise geographic distances between sample sites measured as the shortest distance via water in Google Earth. Mantel tests (Mantel 1967) were performed to test for isolation by distance in GenAlEx v6.1 (Peakall & Smouse 2006). Linear regression was performed in Systat v7.0.1 to estimate variance explained (i.e. $R^2$).

2) Kin aggregation: The parr-fry divergence may have resulted from non-random sampling of the relatively newly emerged fry in family groups (kin aggregations). To explore the potential role of kin aggregation in the parr-fry divergence, mean relatedness (RI estimator, Ritland 1996) was calculated for all parr and fry sample groups in GenAlEx v6.1 (Peakall & Smouse 2006). An ANOVA was performed in Excel to compare the variation in relatedness values for parr groups versus fry groups. A t-test was performed in Systat v7.0.1 to determine if the difference between parr and fry relatedness values was different from zero.
3) Genetic drift: To quantify temporal variation in allele frequency distribution, an AMOVA with 10,000 permutations (Arlequin v3.11, Excoffier et al. 2005) was performed among years on juvenile fish collected in 2006 and 2008 nested within sample sites (11MC, HAG, HEA, RRC, TSA, WIL). The moments based effective population size ($N_e$; Waples 1989) was calculated using $N_e$ Estimator (Peel et al. 2004) to investigate the potential role of genetic drift in the genetic divergence between parr and fry in Eleven Mile Creek, Boucher Creek, and Donald Creek. These sites were selected because they had parr sample groups that contained only age 1+ parr and age 0+ fry which could be used as temporally replicated sample groups. I excluded all parr identified as strays from this analysis.

2.3 Results

After Bonferroni correction, most sample groups did not display significant departures from Hardy Weinberg equilibrium (HWE). For a small proportion of sample groups, the null hypothesis was rejected, but there were no consistent patterns across loci or sample groups (Table 2.1). The fork length histogram of all fish captured at all sampling sites showed a clear bimodal distribution with fry (0+ year old) being less than 60mm and parr greater than 60mm (Figure 2.3).
Figure 2.3 Histogram of juvenile rainbow trout (*O. mykiss*) fork length in 5 mm increments for all Babine Lake, BC sampling sites combined. Arrow indicates the division between fry (≤ 60 mm) and parr (> 60 mm).

The global $F_{ST}$ for all populations is 0.053 (0.048 to 0.058 95% confidence interval). All pairwise exact tests of allele frequency distributions between parr and fry were significant ($p < 0.05$) after Bonferroni correction, an unexpected result which prompted us to further investigate genetic differences between life-stages.

1) Out of 363 parr, 224 (61.7%) were assigned to fry groups (Table 2.2), 124 (34.2%) failed to assign, and 15 (4.1%) were excluded from assignment. Of the fish that were assigned, 94 (42.0%) parr assigned to the fry group in the same tributary in which they were caught, 52 (23.2%) parr assigned to a fry group within the same region, and 78 (34.8%) parr assigned to a fry group from a different region than that in which they were captured. Of the 132 parr that did not assign to the fry group in the same tributary in
which they were captured, the majority dispersed less than 100 km (n = 99, 76.2%), while only 31 (23.8%) dispersed further than 100 km (Figure 2.4). Based on site to site geographic distances, parr dispersed a mean distance of 60.9 km (range: 1.87 km to 233.5 km).

![Dispersal Distance (km) vs Number of Parr](image)

**Figure 2.4** Histogram of dispersal distance (km) of rainbow trout (*O. mykiss*) parr in Babine Lake, BC based on genotype assignment of parr to source fry populations.
Table 2.2 Counts of parr assigned to fry groups using GeneClass 2.0.h. Number of parr assigned and total number of parr collected are listed in parentheses below each parr source code. Geographic regions are highlighted in light grey and self-assigned fish are highlighted in medium grey. Adjacent sites in the table are spatially the closest, in a north to south direction.

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| Parr Capture Location |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
|-----------------------|-----|-----|-----|-----|-----|-----|-----|-----|------|-----|-----|-----|-----|-----|-----|-----|-----|
| NKB (2/6)             |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| NYC (8/11)            |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| BCC (15/28)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| BFC (15/23)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| DJC (7/16)            |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| HEA (23/36)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| SMC (4/13)            |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| 11MC (12/20)          |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| UMT (23/31)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| HAG (12/21)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| RRC (19/30)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| RRC (19/30)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| WIL (16/30)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| CRC (23/31)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| DNC (12/17)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| GWC (13/30)           |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
| SR (20/23)            |     |     |     |     |     |     |     |     |      |     |     |     |     |     |     |     |     |     |
None of the fry were excluded from all the sampled tributaries in the genotype assignment of fry to fry. Of 484 fry, 456 (94.2%) assigned to the fry groups in the same tributary in which they were caught, 5 (1.03%) assigned to a different tributary, and 22 (4.5%) were unassigned. These results support my assumption that the newly-hatched fry do not generally disperse among tributaries.

Parr global $F_{ST}$ before the removal of stray parr was 0.0496 (0.043 - 0.057 95% confidence interval) and 0.0582 (0.052 - 0.065 95% confidence interval) after the removal of dispersed parr. The increase in $F_{ST}$ is consistent with my expectations. The change in pairwise $F_{ST}/(1-F_{ST})$ values between parr and fry groups calculated before and after removal of strays from parr groups was significantly different from zero (T-test $p < 0.001$; Figure 2.5a) with a shift towards greater $F_{ST}/(1-F_{ST})$ values after removal of dispersed parr, indicating that parr and fry groups are more divergent when dispersed parr are removed. Comparisons of pairwise parr $F_{ST}/(1-F_{ST})$ values before and after the removal of strays showed a significant increase in $F_{ST}/(1-F_{ST})$ with the removal of dispersed parr (mean change in $F_{ST}/(1-F_{ST}) = 0.004$; T-test $p < 0.001$; Figure 2.5b). Such a shift indicates that parr dispersal homogenizes tributary populations and decreases genetic divergence.
Figure 2.5 Genetic divergence as measured by pairwise $F_{ST}/(1-F_{ST})$ between Babine Lake rainbow trout ($O. mykiss$) a) between parr and fry groups before and after removal of dispersed parr (T-test $p < 0.001$) and b) between parr groups before and after removal of dispersed parr (T-test $p < 0.001$).
The AMOVA performed with parr and fry collected in 2008 before removal of dispersed parr showed that 1.53% (p < 0.0001) of the genetic variation was attributable to variation among life-stage groups within sample sites, 4.03% (p < 0.0001) was due to spatial variation among sample sites, while 94.44% (p < 0.0001) was attributable to variation among individuals within life-stage groups. The AMOVA performed after the removal of dispersed parr showed that 1.49% (p<0.0001) was attributable to variation among age groups within sample sites, 4.49% (p<0.0001) was due to variation among sample sites, while 94.02% (p<0.0001) was attributable to variation among individuals within life-stage groups. This indicates that dispersed parr are somewhat masking genetic variation among sample sites.

Significant correlation of geographic distance and $F_{ST}/(1-F_{ST})$ values for fry groups was consistent with a pattern of isolation by distance and had an $R^2$ value of 0.16 (Mantel $p = 0.040$; Figure 2.6a). Parr sample groups before removal of dispersed parr also showed a significant pattern of isolation by distance with an $R^2$ value of 0.21 (Mantel $p = 0.010$; Figure 2.6b). Correlation of geographic distance and $F_{ST}/(1-F_{ST})$ values for parr groups after removal of stray parr was also consistent with a pattern of isolation by distance but geographic distance explained a greater proportion of the observed variance in genetic divergence ($R^2 = 0.26$; Mantel $p = 0.020$; Figure 2.6c). The higher $R^2$ value after removal of dispersed parr indicates that dispersed parr diminish the strength of isolation by distance patterns across the system.
Figure 2.6 Scatterplot of pairwise F_{ST}/(1-F_{ST}) values versus distance (Slatkin 1995) for Babine Lake, BC rainbow trout (O. mykiss) from 9 tributaries sampled in 2008. Panel a: fry, Panel b: parr before removal of dispersed parr, and Panel c: parr after removal of dispersed parr. For fry R^2 = 0.16 (Mantel p = 0.040), for parr before removal of dispersed parr R^2 = 0.21 (Mantel p = 0.010), and parr after removal of dispersed parr R^2 = 0.26 (Mantel p = 0.020).
2) Relatedness values for parr ranged from 0.011 to 0.090 and 0.012 to 0.095 for fry. The ANOVA showed no significant difference between parr and fry relatedness values (p = 0.67). Pairwise comparison of fry and parr relatedness showed that the trend follows the 1:1 line (Figure 2.7) and the mean difference between tributary parr and fry relatedness values is not significantly different from zero (T-test p=0.33). Thus there is no evidence for life-stage specific kin aggregation.

![Figure 2.7 Pairwise comparison of Babine Lake, BC rainbow trout (O.mykiss) fry and parr relatedness data (RI estimator, Ritland 1996; T-test p = 0.33). The 1:1 line is shown.](image)

3) The AMOVA to investigate the temporal component of genetic variation between 2006 and 2008 juveniles from the same sampling sites showed that 1.87% (p < 0.0001) of the genetic variation was due to variation among year groups within sampling sites, 1.45% (p < 0.0001) was attributable to variation among sampling sites, and 96.7% (p < 0.0001) was attributable to variation among individuals within year group samples. This
indicates a substantial level of temporal genetic variation within the study system sample sites. My $N_e$ estimates for the three tributaries where $N_e$ estimation was possible were very low: Eleven Mile Creek $N_e = 3.2$ fish (95% CI = 1.9 - 5.5); Boucher Creek $N_e = 25.5$ fish (95% CI = 10.8 - 287.4); and Donald Creek $N_e = 4.0$ fish (95% CI = 2.6 - 6.3).

2.4 DISCUSSION

Rainbow trout, and salmonids in general, display natal philopatry, but the scale at which this is evident varies from system to system (Dittman & Quinn 1996). In some cases it is present at a very fine spatial scale (e.g., Garant et al. 2000), but it can also take a larger geographic scale for these patterns to be detected (e.g., Spruell et al. 1999). Although little research has been done to investigate RBT genetic structure at the lake-level, based on similar studies on salmonids (sockeye salmon in Hendry et al. 1998 and Arctic char in Power et al. 2005) I expected less genetic structure among the tributaries than I observed. The global $F_{ST}$ value observed for Babine Lake RBT (0.053) is more similar to values observed for salmonid populations in separate river systems: for example 0.027 to 0.048 in chinook salmon (Heath et al. 2006), 0.062 in cutthroat trout (Wofford et al. 2005) and 0.063 in bull trout (Spruell et al. 1999). This indicates that the observed $F_{ST}$ is high for a lake-level system. In salmonids, high $F_{ST}$ values such as those I report are indicative of limited gene flow between populations. However, some of the observed genetic structure was actually due to genetic divergence between life-stages within tributaries, as shown by other analyses. Such genetic divergence between life-stages in fish has not been found in any other studies that I am aware of.
There are several possible explanations for the genetic divergence between life-stages in juvenile RBT of the Lake Babine tributaries. The mechanism(s) must be life-stage specific to account for the genetic divergence between parr and fry in all of the sampled tributaries. The three most obvious possible contributing factors are: differential dispersal, differential kin aggregation, and very high genetic drift resulting from the different spawning populations for the two life stages.

Perhaps the most obvious factor that could explain the parr-fry divergence is higher dispersal of the parr relative to the fry. Past sampling efforts in Babine Lake captured no fry or yearling parr in the lake, but did capture older parr (Bustard 1989). Based on this, it seems unlikely that fry are dispersing among Babine Lake tributaries but that older, larger parr may be dispersing via the lake. My genotype assignment showed that not only are substantial numbers of parr dispersing among tributaries, but also the parr dispersal distance could be large, with some dispersing more than 100 km. Interestingly, fry and parr showed a pattern of isolation-by-distance among tributaries, which strengthened after the removal of dispersing parr. Although the majority of parr dispersal was to tributaries that are relatively nearby, the movement of some parr may have been enough to lessen the strength of isolation-by-distance patterns as the movement of only a few reproductive individuals per generation may be enough to obscure genetic differences between populations (Waples 1998). This is consistent with my finding that overall genetic divergence among parr groups was higher after the removal of dispersed parr, which indicates that inclusion of the stray parr in my genetic structure analysis clearly
had a homogenizing effect on the level of genetic divergence among tributaries (Walter et al. 2009). However, the removal of dispersed parr did not affect the divergence between parr and fry groups within tributaries. Although the parr-specific dispersal is novel, it is apparently not contributing to the parr-fry divergence in this system. Furthermore, the high levels of divergence among tributaries indicate that parr are likely returning to and spawning in the tributary in which they hatched. That is, they are not a source of gene flow in the system and do not likely erode the potential for local adaptation.

Secondly, the sampled fish could be closely related. Kin aggregation can prove beneficial when fish school to improve foraging and avoid predation (Quinn & Busack 1985), but aggregation can also be costly in areas where food and cover are scarce (Griffiths et al. 2003). Carlsson et al. (2007) found that in some stream populations of brown trout, closely related individuals are found closer together than more distantly related fish, but that in other streams this pattern does not apply. Although my sampling and analysis should have detected the presence of kin aggregation, I found no evidence that it occurred in the sampled populations. Therefore, kin aggregation is probably not playing a role in the genetic structure of Babine Lake RBT parr and fry.

It seems highly unlikely that genetic drift could be responsible for the genetic divergence between parr and fry in Lake Babine. Since the Lake Babine RBT can spawn more than once, the composition of the spawning population should not change substantially from
one year to the next. However, the AMOVA analysis of temporal replicate samples showed that temporal variation exceeded spatial variation in the system. Furthermore, in the three cases where I could reliably estimate $N_e$, the values were remarkably low (3.2, 4.0 and 25.5), lower than $N_e$ estimates found in other studies ($Oncorhynchus$ spp. in Bartley et al. 1992, brown trout in Jorde & Ryman 1996, and steelhead in Heath et al. 2002). Heath et al. (2002) found that $N_e$ was much smaller than the population census size ($N$) in several populations of steelhead trout, and in general, the $N_e:N$ ratio is very low for salmonids (e.g., Shrimpton & Heath 2003). Although no adult spawner census estimates are available for the three sampled tributaries for which $N_e$ was calculated, some parr and fry production estimates are available. Aside from the Sutherland River, which is suspected of producing 65% of the juveniles in the lake, production estimates range from 0 to 9373 juveniles (Bustard 1989) per tributary. Using RBT mean survival (egg to fry = 0.293 and egg to parr = 0.014, Quinn 2005), mean fecundity values 3,000 eggs per female estimated from Becker (1983), and mean tributary production values (fry = 6309 and parr = 4158, Bustard 1989), I calculated the approximate number of females necessary in each tributary to account for the juvenile production. Although this is a rough calculation, it indicates that, on average, only 53 females would be necessary to account for the observed juvenile numbers in the three tributaries. Heath et al. (2002) reported an average $N_e/N$ ratio of 0.15 for steelhead trout in northern British Columbia. When applied to my female spawner estimates, I got an $N_e$ estimate of 8.12, which is in line with my calculated $N_e$ values. Thus low $N_e$, coupled with probable high variation in reproductive success likely contributes to very high genetic drift in this system,
accounting for the puzzling genetic divergence between fry and parr in the nursery tributaries.

Because low effective population size can play an important role in changes in genetic variability over time (Frankham 2002), it seems likely that small $N_e$ and random genetic drift are controlling the genetic variation divergence between life-stages I am observing. Very low estimates of $N_e$ will lead to very fast genetic divergence by drift and may increase the risk of extinction (Newman & Pilson 1997). Given the high level of drift possible in this system, a pattern of extinction and recolonization events is possible even though I measured high levels of genetic structure. A system characterized by high levels of local extinction and recolonization can be a metapopulation (Frankham et al. 2002). Metapopulations are associated with many negative conservation implications, such as low effective population sizes and loss of genetic diversity (Wang & Caballero 1999). Metapopulations have a source-sink structure and source populations need to be protected (Frankham et al. 2002), but identification of source populations can be difficult. Movement of spawners into tributaries following extirpation would be necessary for recolonization. Because I examined parr dispersal in the system, I am not in a position to determine if a meta-population structure is present in the system.

Overall, this investigation of spatial and temporal structure of juvenile RBT in Babine Lake shows that genetic drift and, to a lesser extent, dispersal play roles in driving the
life-stage specific genetic structure observed in Babine Lake tributaries. My investigation revealed structure detectable at the lake-level, but more interestingly it showed genetic divergence between life-stages (parr and fry) in tributaries. Although dispersal of parr occurs, it did not explain much of the genetic divergence between life-stages. Kin aggregation was also excluded as an explanation for the divergence. Estimates of N_e for tributaries were extraordinarily low, which implies that rapid genetic drift may be causing the observed genetic divergence between life-stages. To fully understand the patterns of genetic divergence in the system an analysis of spawning adults will be necessary. Although it is not often considered or investigated, the potential for highly genetically divergent life-stages may be a more common phenomenon than is currently thought.
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3.0 Adult Rainbow Trout Mixed Stock Distribution in Babine Lake

3.1 Introduction

As a result of high rates of homing, genetic structure develops across the range of many salmon species (Dittman & Quinn 1996) and in many cases these divergent groups are classified as separate stocks for management purposes. In salmonids, many stocks migrate to common rearing grounds and mix (Utter & Ryman 1993) and oftentimes, these fish are harvested as a mixed stock (Utter & Ryman 1993 and Waples et al. 1990). In many cases, fish from the various stocks are not easily identified by morphological characteristics, so management of individual target stocks can be difficult. Restricted harvest of one stock or protection of weak stocks from a particular geographic location can be logistically complex (Waples et al. 1990). Therefore, knowing the relative contributions from each stock to the mixed stock fishery is important to management. Harvest quotas can be set based on underrepresented stocks to avoid overharvest and knowing the harvest composition can influence decisions about season lengths and provide insight into which stocks are affected by a fishery (Milner et al. 1985). Maintenance of genetic health and diversity is important to the continued persistence of populations (Frankham 2003) because the loss of genetic diversity can severely limit the ability of a population to cope with changes in the environment and adapt to new conditions (Reed & Frankham 2003). Therefore, an understanding of mixed stock fisheries structure that leads to appropriate management is critical for the overall health and sustainable management of a fishery.
Mixed stock fisheries are often dominated by a particular stock with lower contributions from other stocks (Krueger et al. 1999, Milner et al. 1995, Seeb & Crane 1999), but relatively equal contributions from stocks is also possible. Genotype assignment may be used to determine the composition of mixed stock fisheries and the dispersal of fish (Castric & Bernatchez 2004, Milner et al. 1985, Utter & Ryman 1993, Waples et al. 1990). Patterns of dispersal and distribution in fish can be complex and variable over the course of their life. Many factors such as bathymetry (Sammarco & Andrews 1989), flow regimes (Crisp & Hurley 1991), physical factors such as dissolved oxygen levels (Rowe & Chisnall 1995), habitat availability (Jowett et al. 1996), and food availability (Walters 2000) can influence the dispersal and distribution of fish in a system. Patterns of distribution may vary throughout the year as well, for instance fish will be distributed in a stream differently during the spawning season than at other times of year (Wilson et al. 2004). Kin aggregation, which can confer benefits or disadvantages (Carlsson et al. 2003, Griffiths et al. 2003, Quinn & Busack 1985), can be a factor in the non-random distribution of fish. Additionally, differential habitat use, or habitat partitioning, may drive some patterns of distribution. Habitat partitioning may be inter- or intraspecific and often results from competition for food resources or available habitat (George & Hadley 1979, Matthews & Hill 1980, Ross 1986).

Like other Pacific salmonids, rainbow trout (RBT, Oncorhynchus mykiss) display natal philopatry, but unlike other Pacific salmon they are iteroparous and can return to spawn year after year (Quinn 2005). Structure has been found among RBT populations at the
regional and within-drainage level (Krueger et al. 1999, Narum et al. 2006, Chapter 2) and there is the possibility for local adaptation and divergence between populations, which makes the species a candidate for genotype assignment. *O. mykiss* exist as both anadromous and resident forms. Anadromous fish are known as steelhead and spend a portion of their life at sea where they can attain large body sizes. Resident fish are referred to as rainbow trout and spend their entire lives in fresh water, but may migrate within that system. These resident RBT commonly spawn in tributaries of lakes or rivers in the spring. The fry and parr rear in the tributaries for several years before moving into the lake or river to rear until maturity. Adults also reside in the lake and return to tributaries to spawn, but the patterns of distribution while in the lake are not well understood.

In this study I examined the distribution of adult resident RBT in Babine Lake relative to their natal tributaries. Other studies have found non-random distribution of Atlantic salmon in a lake (Potvin & Bernatchez 2001) and preferential dispersal of Atlantic salmon and brook charr into nearby streams (Castric & Bernatchez 2004). Therefore, I suspect that dispersal of adult fish is not random, and my hypothesis is that adults originating from the same tributary are not distributing randomly throughout the lake. Specifically, I predict that adult RBT will remain in zones of the lake that are spatially proximal to their tributaries of origin. To address this question, I used microsatellite genotype assignment to determine the likely source breeding population of adult RBT collected from throughout the lake. My previous findings (Chapter 2) of substantial
genetic structure among the juvenile RBT in 18 tributary populations provides us considerable power for genotype assignment of the lake-caught adult RBT. Using the source population assignment data I tested for non-random distribution of the adult fish captured in Babine Lake. An investigation into the dispersal and distribution patterns of adult RBT in Babine Lake will contribute to a better understanding of distribution patterns of resident fish that display natal philopatry and is an important step to improved management of this exploited resource.

3.2 MATERIALS AND METHODS

Study Site

In Babine Lake, resident RBT reside in the lake as adults and spawn in its tributaries. For this study, RBT in Babine Lake and its tributaries were sampled along with RBT from Nilkitkwa Lake (located just north and downstream of Babine Lake) and a segment of the Babine River known as Rainbow Alley that connects Babine and Nilkitkwa lakes (Figure 3.1). Babine Lake, located in northwestern British Columbia (Figure 3.1), is a narrow, long (>177km) lake that supports the largest recreational RBT fishery in the region and First Nations food fisheries. Therefore, the Babine Lake rainbow trout fishery is both economically and socially important to the region.
Figure 3.1 Map of Babine Lake, British Columbia, Canada showing the location of adult rainbow trout (*Oncorhynchus mykiss*) sampling zones. Zones are marked by black lines. Zone S (marked with a circle) adults were sampled while entering the mouth of the Sutherland River.
Sample Collection

To collect adult fish from throughout Babine Lake and to minimize sampling bias, adult rainbow trout were collected in the summers of 2007, 2008, and 2009 (Table 3.1) by angling, gill netting (75m variable mesh), and as by-catch from a sockeye salmon (*O. nerka*) beach seine fishery. Along with fork length (mm), a small adipose fin clip was collected from each fish and was stored in either 95% ethanol or RNAlater for subsequent DNA extraction. Babine Lake, Nilkitkwa Lake, and a portion of the Babine River were divided into 12 zones (Figure 3.1) and the zone in which each fish was captured was recorded along with the date. Most adults were sampled during the summer and early fall, however, some adult RBT were sampled at the mouth of the Sutherland River (Zone S) in the late spring. It is assumed that they were entering the river to spawn. Juvenile rainbow trout were collected from twenty Babine Lake tributaries in 2006 and 2008 (Figure 2.1) and genotyped at 13 loci for a previous study (see Chapter 2) and those genotypes served as the basis for the presumed source populations. As in Chapter 2, the tributary sample sites were placed into geographic regions: Lower Babine (NKB, NYC, BCC, BFC, DJC, BBR), North (HEA, 11MC, 5MC, TSA), Main (UMT, HAG, RRC, WIL, TAC), South (CRC, DNC, GWC), and Sutherland/ Duncan (DCA-DCC and SRA-SRI) as in Chapter 2 (Figure 2.1).
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<td>68</td>
<td>160 - 548</td>
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<tr>
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<td>601</td>
<td>160 - 865</td>
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</table>
DNA Extraction and Microsatellite Genotyping

DNA was extracted from 601 adult RBT using the column-based plate extraction method described in Elphinstone et al. (2003). All individuals were genotyped at thirteen microsatellite loci that were previously developed for RBT and other Pacific salmonids: Ots3 and Ots4 (Banks et al. 1999) with 11 and 13 alleles respectively; Ots243, OtsG401, OtsG43, OtsG253b, OtsG249, and OtsG83b (Williamson et al. 2002) with 4, 17, 14, 26, 24, and 25 alleles respectively; RT191, RT212, and RT561 (Spies et al. 2005) with 23, 29, and 9 alleles respectively; Omy325 (Olsen et al. 1996) with 29 alleles; and ONE101 (Olsen et al. 2000) with 13 alleles. As described in Chapter 2, polymerase chain reaction (PCR) conditions were optimized for each locus and thermocycler protocols used locus specific annealing temperatures. PCR product fragment size was determined using a LiCor 4300 DNA analyzer and Genelmagr software (Scanlytics, Inc.).

Genetic Analyses

All microsatellite loci were tested for departures from Hardy-Weinberg equilibrium using 10,000 dememorisation steps, 100 batches, and 5000 iterations per batch in GenePop v4.06 (Rousset 2007) with juvenile populations and significance was adjusted for multiple tests using the Bonferroni method (Rice 1989). Adult RBT were not tested for departures from Hardy-Weinberg equilibrium because, having originated from many tributary populations, they violated the assumption of a single, closed population.
To determine which tributaries adult RBT are spawning in, and therefore are likely originating from, genotype assignment of adult fish to tributary populations was performed with GeneClass 2.0.h (Piry et al. 2004). Adult RBT were assigned to juvenile tributary populations to link adults to their offspring. Juvenile RBT were used as source populations because a larger number of juveniles could be collected in tributaries than if adult spawners were collected and several life-stages of juveniles were captured (see Chapter 2) which should mean that a representative sample was obtained. A two-step process was used to perform the assignment. First, a probability computation utilizing Monte-Carlo resampling (Paetkau et al. 2004) was used to exclude fish: If an individual adult had less than 10% probability of being assigned to any juvenile sample group it was likely to belong to an unsampled tributary population, and was excluded from further analyses. Secondly, the remaining adults were assigned to fry sample groups with a rank-based method (Rannala & Mountain 1997). Resampling was not utilized and the five most likely tributary populations of origin were ranked. The majority of fish (62.8%) had a nine-times or greater likelihood ratio between the first and second ranked tributaries; however, to determine the sensitivity of my analysis to my choice of assignment threshold, I performed a sensitivity analysis where I varied the assignment probability threshold and evaluated the effect on the number of fish successfully assigned (Figure 3.2). Because designating a threshold value in the range of 3x to 9x would not greatly change the number of assigned individuals, the value of 4x was selected as it has been used in other studies (e.g., Beneteau et al. 2008). The majority of captured adults were collected from Babine Lake throughout the summer. I did, however, have 33 samples collected at the mouth of the Sutherland River as the fish were presumably entering the
tributary to spawn. Therefore, assignment of these fish was used as a formal test of the efficacy of the genotype assignment.

![Graph showing the ratio of probabilities of assigning to the first-ranked tributary vs the second-ranked tributary](image)

**Figure 3.2** Sensitivity analysis of number of Babine Lake, BC rainbow trout (*O. mykiss*) adults assigned to a tributary when varying ratios of the probability of assigning to the first-ranked tributary vs the second-ranked tributary are used. White bar indicates the total number of adults.

To determine if the distribution of fish throughout the lake was random, \( \chi^2 \) analyses were performed. Expected values for each zone were determined by multiplying the number of fish captured in a zone by the lake-wide proportions of fish assigned to each tributary. Observed values were the counts of fish in each zone that assigned to each tributary. Because several tributaries had too few adult RBT assign to them to perform a \( \chi^2 \) analysis for each zone, these analyses were performed with two groupings of sampling zones. Sampling zones Aa, A, B, C, and D were combined and zones E, F, G, H, I, J, and K were combined. To determine if adult RBT in all regions are, on average, equally distant
from their natal tributaries, I tested for differences in the mean dispersal distance among the five regions using a Kruskal-Wallis one way analysis of variance (because the dispersal distances were not normally distributed) in Systat (v7.0.1).

To investigate whether adults of various sizes are dispersing equal distances, I divided fish into groups based on fork length and calculated the mean dispersal distance for each group. Because not all data were normal, I used a Kruskal-Wallis one-way analysis of variance in Systat (v7.0.1) to determine if the median dispersal distance was equal among fish of varying size. A Spearman’s rank order correlation was performed in Systat (v7.0.1) to determine if dispersal distance was correlated with body size.

To explore the potential role of relatedness in impacting the pattern of distribution, I calculated mean relatedness (RI estimator, Ritland 1996) for all zones and for the overall adult RBT population in GenAlEx v6.1 (Peakall & Smouse 2006). A t-test was performed in Systat v7.0.1 to determine if the difference between sampling zone and lake-wide relatedness values was significant.

3.3 Results

After Bonferroni correction, most sample groups did not display significant departures from Hardy Weinberg equilibrium (HWE). For a small proportion of sample groups
(0.65%), the null hypothesis was rejected, but there were no consistent patterns across loci or sample groups.

Of 601 adult fish, 60 (9.98%) were excluded from assignment in the first step, 391 (65.1%) fish were successfully assigned to tributaries (Table 3.2), and 150 (25.0%) fish failed to assign. Zones A and I had the highest number of excluded assignments (n = 18 = 30.6% and n = 11 = 19.0% respectively), perhaps indicating that there is an unsampled tributary source population in that region. Overall, however, it is likely that I sampled the majority of RBT production tributaries since relatively few fish were excluded from assignment to tributaries. Of the fish that were assigned, 80 (22.3%) adults assigned to a tributary that drains into the zone in which they were captured and 48 (13.4%) adults assigned to a tributary that drains into a zone adjacent to the zone of capture. The remaining 231 (64.3%) adults assigned to a tributary that drains into a further zone. Based on the distance from the source tributary to sampling zone mid-point, adults moved 0.1km to 165km with an mean distance of 60km (SEM = ± 2.5). Of the 391 assigned adults, the majority dispersed less than 101 km (306 fish, 78.3%), while only 85 fish (21.7%) moved further than 101 km (Figure 3.3). In all 5 regional groups, the number of dispersing fish decreased as distance from zone of capture increased. For the North and Lower Babine regions, the majority of adults dispersed less than 50 km and there was a sharp decline in the proportion of fish that dispersed further than 50 km. While the Sutherland, Main, and South regions experienced a decline in proportion of fish that dispersed as distance from zone of capture increased, the decline was more
gradual with the majority of fish dispersing less than 100 km. Of the 33 samples collected at the mouth of the Sutherland River, one fish failed to assign anywhere. The remaining 32 assigned to the Sutherland River (and Duncan Creek, a tributary of Sutherland River), which validates my genotype assignment protocol.
Table 3.2 Proportion of adults from each sampling zone assigned to tributaries and excluded from all tributaries using GeneClass 2.0.h. Number of adults assigned is listed in parentheses below each sampling zone code. Geographic regions are separated by horizontal lines. Adjacent tributaries in the table are spatially the closest, in a north to south direction.

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<th>Zone B (16)</th>
<th>Zone C (20)</th>
<th>Zone D (20)</th>
<th>Zone E (31)</th>
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Figure 3.3 Distance (km) from tributary of origin for rainbow trout (*O. mykiss*) adults in Babine Lake, BC by region.

Based on $\chi^2$ analysis, the distribution of adult RBT in the two groupings of sampling zones were significantly different from random at the $p = 0.05$ level, indicating that adult fish are not randomly distributed throughout the lake. For the Kruskal-Wallis one-way analysis of variance, the null hypothesis was rejected ($p < 0.001$) indicating that adult RBT are not equally distant from their natal tributaries.

Overall, mean dispersal distance increased with body size (Figure 3.4). The null hypothesis was rejected ($p < 0.001$) for the Kruskal-Wallis one-way analysis of variance which indicates that there are significant differences in the dispersal distances of fish depending on their size. The Spearman’s rank order correlation indicated that body size is positively correlated with dispersal distance ($r_s = 0.750$).
Figure 3.4 Mean dispersal distance for adult rainbow trout (*O. mykiss*) of various body sizes in Babine Lake, BC.

Relatedness values for adults assigned in a sampling zone ranged from -0.004 to 0.043 and the overall lake relatedness value was -0.001. The t-test showed that there is not a significant difference (*p = 0.086*) between lake-wide relatedness and relatedness of adults in the zones.

3.4 DISCUSSION

My analyses showed that the distribution of adult RBT throughout Babine Lake is not random. There are several mechanisms by which the distribution of fish might not be random throughout their habitat. The first is that the dispersal abilities of all the fish are not equal. Secondly, kin aggregation and relatedness of individuals could be affecting
distribution patterns. A third possibility is that habitat partitioning and differential resource use is causing non-random distribution.

The ability to disperse in a system can be impacted by many factors (Crisp & Hurley 1991, Rowe & Chisnall 1995, Sammarco & Andrews 1989, Walters 2000). In Babine Lake, it appears that the size of a fish has the most impact on its dispersal ability. The positive relationship between fork length and distance from the tributary of origin indicates that the size of a fish is an important predictor of how far it will be able to disperse in the lake. Jenkins et al. (2007) found that among active dispersers, greater dispersal distances were attained by the larger individuals. Because size and age are related (Kimura 1980), it is possible that dispersal distance is driven by the age of the fish. Based on length and age data for Babine Lake RBT, the fish sampled for this study range from 3 to 8 years of age. Although it is not possible to determine the age of my collected fish more precisely than to a range of years using the length and age data, it is possible that some of the longest dispersal events measured in this study may have been undertaken by older fish. One possibility is that the older fish would have had a longer time to disperse than the younger fish. Although Babine Lake is a large lake (>177km), O. mykiss are capable of migrating very long distances (Busby et al. 1996), so it is not improbable that adults from the various tributaries have dispersed throughout the lake.
Although RBT from various tributaries did disperse to parts of the lake far from their tributary of origin, there was a general trend that fish from tributaries in the North and Lower Babine regions dispersed mostly to northern sampling zones, whereas fish from the Main, South, and Sutherland/Duncan regions dispersed to zones in all parts of the lake. This could be indicative of differential use of resources or differences in the habitat. de Leeuw (1990) noted that adult RBT congregate at the mouths of Fulton River and Pinkut Creek, both sites of artificial spawning channels for sockeye, when sockeye salmon fry emigrate from the tributaries. Patterns of adult RBT distribution may be influenced by availability of food resources. In addition, if prey choice varies with predator fish size (George & Hadley 1979), patterns of distribution may be influenced by the availability of the preferred prey. Larger RBT are often piscivores, so availability of fish prey may have a different influence on the distribution of RBT based on size.

Habitat preference and availability have also been shown to drive habitat partitioning among species (Matthews & Hill 1980, Ross 1986). However, examples within species are less common. Northern sampling zones contained adult RBT from a greater proportion of tributaries than southern sampling zones, which could be indicative of high quality habitat in the northern region.

Kin aggregation can impact the distribution of fish in a water body (Carlsson et al. 2003, Griffiths et al. 2003, Quinn & Busack 1985), but there is little evidence that kin aggregation is playing a role in the distribution patterns of RBT in Babine Lake. Calculated levels of relatedness were very low among adult RBT in a sampling zone.
Values of 0.0625 indicate relatedness at the level of first cousins (Ritland 1996) and all mean relatedness values for sampling zones were lower than this, indicating that there were not substantial levels of relatedness among adults in the sampling zones. In addition, RBT that assigned to the same tributary were generally captured in several different lake zones, so there was no overall pattern of potentially related fish aggregating together in the lake.

Currently, Zone K in Babine Lake is closed to recreational fishing. This regulation was implemented to protect fish that spawn in the Sutherland River and Duncan Creek, which drain into Zone K. My results show that adult fish from the Sutherland River and Duncan Creek constitute the majority of adult fish that were captured throughout the lake. Bustard (1989) estimated that the Sutherland River and Duncan Creek had the highest juvenile production rates, which agrees with the high number of Sutherland/ Duncan adult RBT caught in the lake. In addition, Sutherland/ Duncan adult RBT were captured in almost every sampling zone in the lake which shows that they can disperse substantial distances. In fact, 85% of RBT caught in Zone K and 62% of RBT caught in other zones of the lake originated in the Sutherland/ Duncan. Because sport angling was the predominant method of capture for the RBT in my study, RBT from Sutherland/Duncan are likely exploited at high rates. The fact that the majority of RBT captured were Sutherland/Duncan fish shows that those fish are abundant throughout the lake. This could indicate that closure of a portion of the lake is not necessary to protect this stock since they are distributed everywhere. However, the large numbers of Sutherland/
Duncan RBT in the system could be the result of the restricted recreational fishing. Some Sutherland/Duncan fish were sampled over 100 km from their source tributary and Sutherland/Duncan RBT were distributed throughout the lake. The mean size of Sutherland/Duncan RBT in Zone K was 345 mm and the mean size of Sutherland/Duncan RBT in the rest of the system was 422 mm. These RBT may be more robust than others in the system and it appears that the smaller Sutherland/Duncan RBT are remaining in the closed section, so it is also possible that protecting them from recreational angling in part of the lake is giving them an advantage over other groups of RBT in the system.

Based on my assignment, the other tributaries contributed far fewer RBT (0.2% to 4.7% per tributary) to the overall population than Sutherland/Duncan (65.7%), so it is possible that those tributaries are more in need of additional protection. Perhaps the non-Sutherland/Duncan tributary stocks have declined because they have been exposed to higher fishing pressure after the closure of the southern part of the lake to recreational fishing. Bustard (1989) had estimated lower RBT production for these tributaries, therefore the lower number of adults from these tributaries relative to Sutherland/Duncan may be normal. While collecting juveniles, I did not sample in such a way that I can estimate production values or juvenile abundance. Consequently, I cannot compare current production values to older values to determine if juvenile production has decreased over time. An evaluation of current tributary production values may be beneficial for management objectives.
Overall, my analysis showed that RBT in Babine Lake are not dispersing randomly throughout the lake after leaving their tributaries of origin. Kin aggregation is not a likely cause of the dispersal patterns, but food availability and dispersal ability are likely more influential on adult distribution throughout the lake. Interestingly, stocks from the northern part of the lake are distributed relatively close to their tributaries of origin, while stocks from the southern portion of the lake are distributed throughout the lake. Further investigation into the factors contributing to the observed differential dispersal patterns is important for both the conservation and management of Babine Lake RBT as well as for a better understanding of the processes that influence distribution and mixed stock composition of fisheries.
3.5 References


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4.0 General Discussion

Many researchers have noted that over time reproductive isolation and differential selective pressures can result in local adaptation in populations (e.g., Taylor 1991, Waples 1991). Populations must be sufficiently reproductively isolated for local adaptation to occur (Aspinwall 1974). Measuring reproductive isolation can be difficult; therefore neutral genetic markers are often used to estimate levels of gene flow and dispersal (Slatkin & Barton 1989). Characterizing gene flow can be complicated by differential dispersal at different life-stages. Although individuals may be dispersing, they are not contributing to gene flow unless they successfully reproduce. Thus there are fundamental differences between the ecological and evolutionary effects of dispersal of adults versus juveniles. Reproductive isolation or limited gene flow also leads to genetic divergence and divergence between populations allows for distinctions to be made between groups of organisms and provides the means for management tools such as genetic stock identification and mixed stock fishery analysis.

Salmonids demonstrate natal philopatry, or homing (Dittman & Quinn 1996). As a result of high rates of homing (Quinn & Fresh 1984) genetic structure may develop across the range of a species (Dittman & Quinn 1996). Although there is generally structure in salmon populations, genetic structure at the lake level has been investigated in only a few systems. When levels of homing are high and genetic divergence between groups is strong, populations of salmonids may become adapted to their local environment. Local
adaptation has important implications for conservation and management because locally adapted populations represent evolutionarily significant units (ESUs) that hold valuable genetic variation, critical for long-term viability (Dodson et al. 1998).

My objectives in this study were to investigate the role of life-stage specific dispersal on lake-wide genetic structure among rainbow trout juveniles in tributary habitats and to examine the distribution patterns of adult rainbow trout throughout Babine Lake. Chapter 2 addresses the role of life-stage specific dispersal and genetic drift on lake-wide genetic structure, genetic divergence between life-stages, and metapopulation structure. Using genotype assignment of adult rainbow trout to tributary source populations, Chapter 3 investigates the dispersal and distribution of adults in Babine Lake. These two chapters provided the opportunity to study dispersal of rainbow trout in both juveniles and adults and gain a better understanding of the effect of dispersal at multiple life-stages on evolution and conservation.

Dispersal is common in this system and is a life-history strategy used by salmonids in general (Quinn 2005). I found evidence that rainbow trout parr are dispersing to other tributaries, and in some instances dispersing parr appear to be lowering the levels of genetic divergence between life-stages and weakening the detected patterns of isolation-by-distance. There was no evidence of fry dispersal among tributaries, which was not surprising given that Bustard (1989) found no evidence of RBT younger than 2 years in
the lake itself. Adult RBT in the system disperse as well. Adult and sub-adult dispersal occurs when RBT leave their natal tributaries to reside in the lake. Adult RBT from northern tributaries were distributed more in the northern regions of the lake, but adults originating in middle and southern tributaries were distributed throughout the lake. Because of this and the density of sampled tributaries in the northern portion of the lake, adults from northern tributaries had a greater proportion of fish that moved less than 100km. Although the overall trend was a decrease in the number of dispersers with increasing distance from source tributary, the decline was more sudden in northern tributary fish than in adults from more southern tributaries. Parr and adult RBT dispersal is similar in that a greater proportion of individuals dispersed to nearby areas rather than dispersing long distances.

While dispersal plays an important role in this system, it is not the main driving force in the unusual genetic divergence between life-stages I observed. Investigation of kin aggregation did not indicate that it was affecting the patterns of divergence. Remarkably low effective population size and the resulting high levels of random genetic drift are likely causing the observed genetic divergence between life-stages as well as temporal variation in the system. Therefore, it seems possible that tributaries may be undergoing a pattern of extinction and recolonization events such as those in metapopulations. Investigation of distribution of adult RBT in the system showed that few adults assigned to some tributaries. While my adult samples are not representative of census or effective
population sizes for tributaries, the low number of assignments to some tributaries does fit with the possibility of a metapopulation structure in the system.

Overall, this study has shown that life-stage specific dispersal and effective population size play an important role in the development of lake-wide genetic structure and that proper management is critical to the continued viability of such populations.

4.1 MANAGEMENT

Loss of genetic diversity can severely limit the ability of a population to cope with changes in the environment and adapt to new conditions (Reed & Frankham 2003). Because there is a high level of divergence among the tributary populations in Babine Lake, there is a high level of genetic diversity, perhaps signifying local adaptation, present in the system. Therefore management decisions that provide for the long-term viability and conservation of all tributary populations is important.

The Sutherland River and Duncan Creek are estimated to produce over 65% of juvenile rainbow trout in the lake (Bustard 1989) and based on my assignment results, the majority (65.7%) of adult rainbow trout sampled originated in those tributaries as well. Because my samples were obtained largely by angling, not only by us, but also by local fishermen and angling guides, it indicates that these fish are susceptible to high recreational fishing pressure. In an effort to protect fish that spawn in the Sutherland
River and Duncan Creek, the southern portion of Babine Lake, Zone K, has been closed to recreational fishing. Adult fish from these tributaries were caught in almost every sampling zone in Babine Lake and Nilkitkwa Lake. Sutherland/Duncan fish made up the majority of fish caught in Zone K and the rest of the lake. While the closure of Zone K has not prevented the exploitation of all Sutherland/Duncan fish, it may still have a beneficial impact on the populations originating in those tributaries. Based on this study, it is not possible to determine the impacts that recreational fishing in Zone K would have on Sutherland/Duncan fish, but the presence of this closed zone may act as a refuge for some of those fish.

Analysis of juveniles in Babine Lake tributaries showed low effective population size and the possibility for metapopulation structure. Low $N_e$ in tributary populations may result in a loss of genetic diversity in the system as a result of random genetic drift and may increase the risk of extinction (Newman & Pilson 1997). Metapopulation structure can lead to lower $N_e$, like I see here, and can lead to a loss of genetic diversity (Wang & Caballero 1999). However, the source-sink structure of metapopulations can prove to be very challenging for management. Identification of source populations is critical for protection of the whole system, but that identification can prove difficult.
4.2 Future Work

To expand on my findings, an analysis of spawning adults would be a logical and important next step in examining the genetic structure in the system. To strengthen the understanding of adult distribution in the lake, an adult tagging study would allow for an investigation of seasonal movements of rainbow trout in the system.
4.3 REFERENCES


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