

**Reproduction in the wild: Linking individual life history strategies to
lifetime reproductive success**

A Dissertation Outline Presented

by

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Introduction

Relating life history strategies to individual fitness, specifically reproductive success, in naturally reproducing populations is at the core of understanding the interrelation between ecology and evolution. Successful life history strategies contribute underlying genotypes and their expressed phenotypes to future gene pools. Thus demographics, optimized at the individual level through selection, links to evolution through time.

Understanding the influence life history strategies have on demographics requires a measurement of individual fitness. Fitness can be defined as the ability to pass on genes (Hedrick 1984). Individual lifetime fitness would then be defined by the survival and reproduction of offspring as measured through the number of grand-offspring produced. One potential method to increase lifetime fitness would be to increase lifetime reproductive success. Lifetime reproductive success of an individual is defined as the number of recruits to the following generation that the individual produces over its entire lifespan (Clutton-Brock 1988, Newton 1989).

Longitudinal studies measuring lifetime reproductive success of identifiable individuals offer several advantages over traditional cross-sectional surveys (Clutton-Brock 1988, Newton 1989). First, they combine the two main components of individual performance, survival and reproductive success, into a single measure. This accounts for any tradeoffs that might exist between reproduction and survival (Partridge 1988, Moyes

et al. 2006, Hanski *et al.* 2006). Second, they allow for the comparison of total fitness among different life history strategies (Clutton-Brock & Pemberton 2004). And third, they are less affected by short-term changes in the environment or individual performance, and thus reduce the variance in breeding success (Clutton-Brock & Pemberton 2004).

Historically, research linking life history strategies to lifetime reproductive success has focused on species that are easy to capture and observe. This was in large part due to logistical, technological, and budgetary constraints. These species, mostly birds (Newton 1989) and mammals (Clutton-Brock 1988), typically display determinate growth, high adult survival, and low fecundity. In most cases at least one of the parents is identifiable from observational data (Kruuk 2004), and many of these populations persist in a closed environment (Clutton-Brock 1988, Newton 1989). This allows for a more complete population census and eliminates the need to account for immigration and emigration. Additionally, pedigree reconstruction is simplified and thus more readily accomplishable compared to species living in open systems and displaying no parental care.

Lifetime reproductive success data from these species, while providing a critical contribution to our understanding of how populations work, represent characteristics from only a small portion of the life history/population dynamics landscape (Stearns 1976). In order to more fully understand the influences of life history strategies and consequences for fitness, there is a need to conduct similar studies on species from other parts of life history space. I propose to study a naturally reproducing population of lotic brook trout (*Salvelinus fontinalis*), characterized by indeterminate growth, size related

fecundity, relatively high mobility, cryptic breeding, and low survival. The focus of the study will be on the causes and consequences of life history strategy on reproductive success (Figure 1), with the following main objectives: 1) Investigate patterns in breeding dispersal among the sexes and determine its influence on population structure and reproductive success. 2) Evaluate patterns of mate choice and their relationship with life history strategies. 3) Determine if differing life history strategies result in equal lifetime reproductive success. 4) Investigate if successful life history strategies are heritable traits.

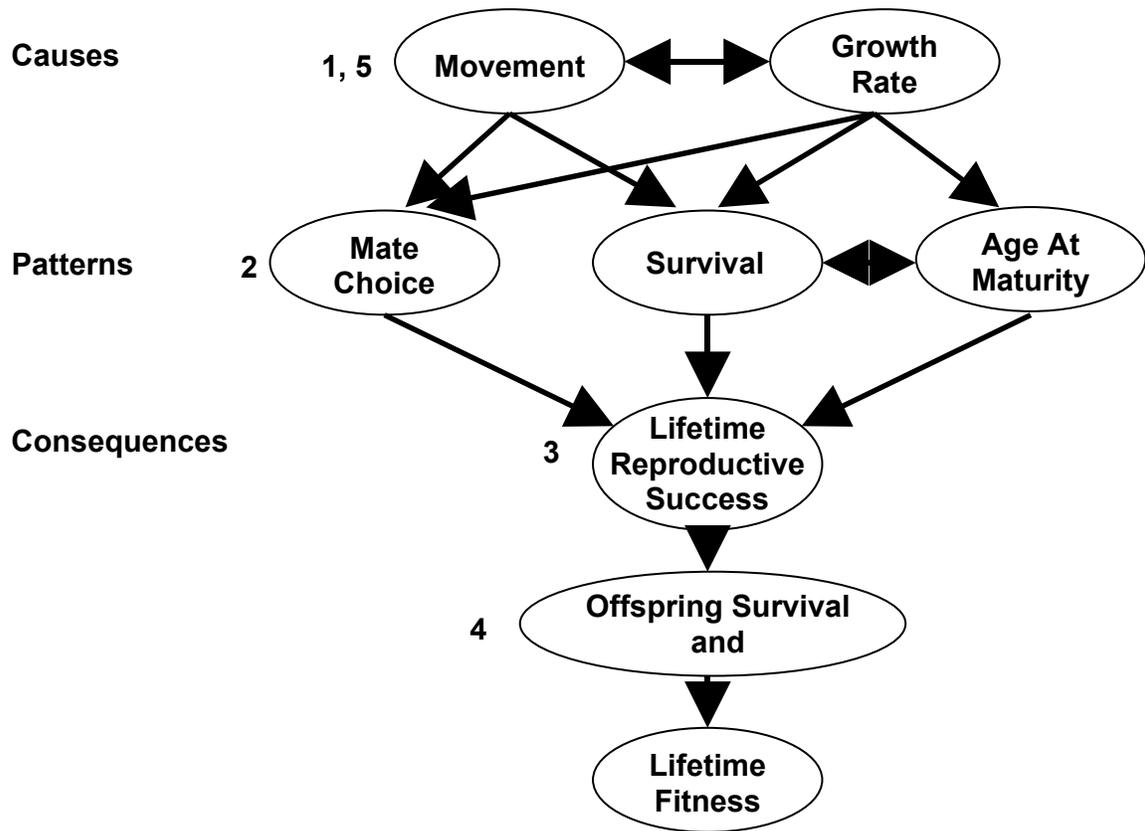


Figure 1: Flow chart depicting the causes and consequences for patterns determining reproductive success. Numbers one through five indicate dissertation chapter involving the adjacent variable.

Background on Brook Trout Life History

A great benefit of using a salmonid as a focal species is the extent of prior research that has been conducted on various aspects of their life history. Below I summarize data for morphology, growth, spawning, female reproductive strategies, male reproductive strategies, mate choice, and population structuring, focusing primarily on brook trout when possible.

Reproductive Morphology

Brook trout (*Salvelinus fontinalis*), are freshwater stream fish characterized by indeterminate growth, size related fecundity, relatively high mobility, cryptic breeding, and low survival. Brook trout reproduce in the fall utilizing a site-based competitive mating system (Blanchfield & Ridgway 1997). Mature males develop secondary sexual characteristics which consist of a deepening of the body, a hooking of the jaw forming a kype, a development of a hump on the back just posterior to the head, and a change in pigmentation to bright red or orange along the lower sides and a whitening of the pectoral, pelvic and anal fin margins (Vladykov 1956). All characteristics become more prevalent as males become larger (personal observation). There is a clear dimorphism between mature males and mature females, with females acquiring none of the male characteristics, but instead displaying a swelling of the ovipositor, and a protrusion of the eggs from the sides and abdomen when they are ripe (Vladykov 1956).

Growth

Brook trout growth rates have been reported as differing between mature males and females in both the summer and winter seasons. Hutchings (2006) reported that male growth rate was nearly twice that of female from June to October, while female growth rate was nearly three times that of male from October to June. He hypothesized that females allocated more energy to gonadal tissue during the summer months in an effort to increase egg development, whereas males allocated more energy to skeletal growth in an effort to maximize size. Data supporting this hypothesis is demonstrated by the significantly greater percentage of gonadal lipids out of total lipids for females (19%) compared to males (8%) recorded in the fall (Hutchings *et al.* 1999). Hutchings (2006) further hypothesized that the decreased growth rate experienced by males from October to June could be attributed to the fact that post-reproductive males lose significantly more lipids than post-reproductive females (Hutchings *et al.* 1999), and thus allocate more energy to lipid reserves than skeletal growth.

Hutchings (2006) also reported an increase in survival for individuals experiencing an increased growth rate for the previous year, but no correlation between survival and growth experienced the previous summer. This suggests that winter and early spring are the seasons when growth has the greatest impact on survival. This is supported by data showing winter months having the highest mortality rate (Hutchings 1993, Petty *et al.* 2005) (but see (Carlson & Letcher 2003)).

Genetic variation present in salmonid size attributes has been shown to contain a heritable component. In a study on hatchery-reared Atlantic salmon, Jonasson (1993) observed significant heritabilities in both length and weight. The strength of heritability differed between mothers and fathers, with values being higher (0.39 and 0.36) for

mothers compared to fathers (0.10 and 0.16). Garant et al (2003) reported heritabilities ranging from 0.57 to 0.27 for a transplanted population of Atlantic salmon reared in a natural habitat. Observed differences were credited to life history strategy of the father (precocious vs. multi-sea winter) and environmental variance introduced by rearing habitat (stream vs. river).

Spawning

Spawning occurs in the fall, usually within a very condensed timeframe.

Blanchfield and Ridgway (1997) reported that 58% and 84% of brook trout spawning in an Ontario lake occurred within an approximately 15 day window for the 1994 and 1995 spawning seasons, even though fish were captured around the spawning area for approximately 63 days, and arrived approximately 25 days before the onset of spawning. Males arrive at the spawning grounds prior to females (Blanchfield & Ridgway 1997, Baril & Magnan 2002), and larger males have been reported as arriving earlier than smaller males (Baril & Magnan 2002). Males become ripe (expression of milt for males, and eggs for females with gentle pressure to the abdomen) earlier than females.

Blanchfield and Ridgway (1997) reported that prior to the onset of spawning only one female out of 76 was found to be ripe, compared to $86\% \pm 16\%$ for males.

Female Reproductive Strategies

Female brook trout demonstrate a variety of ways to increase reproductive success. With the onset of spawning, females select and compete for areas in which to construct redds. For lotic populations, these areas are typically in first- and second-order headwater tributaries, and possess physical attributes consisting of medium substrate (3-20 mm), and strong upwelling of groundwater (Essington *et al.* 1998). Similar redd site

characteristics were reported for lacustrine brook trout populations (Ridgway & Blanchfield 1998), where upwelling of groundwater was the most important characteristic, but these sites also displayed a higher conductivity than random sites (Blanchfield & Ridgway 1997). Competition for these sites by females has been demonstrated by replacement of removed females in an average time of 12 ± 7 minutes, with visitation to the site by multiple females before dominance was established in three out of seven removal trials (Blanchfield & Ridgway 1997).

Additional evidence for female spawning site competition is the superimposition of redds. Essington et al (1998) reported that in a Minnesota stream, 53% of spawning female brook trout superimposed redds. Blanchfield and Ridgway (1997) reported that for two years of spawning only 19 out of 60 spawning sites were used both years, with 50% of spawning activity occurring in eleven of those sites. Additionally, more than half of redd sites were used by three or more females (Blanchfield & Ridgway 1997). Larger females spawn earlier than smaller females (Blanchfield & Ridgway 1997, Blanchfield & Ridgway 2005). Delayed spawning by smaller females may be a strategy to avoid superimposition by larger females (Blanchfield & Ridgway 2005). Evidence for this comes from the positive relationship between the depth of a redd and female brook trout length (Blanchfield & Ridgway 2005). This relationship has also been observed in other salmonid species (Vandenberghe & Gross 1984). Therefore redd superimposition by smaller females on larger female redds will not have as great an impact on egg mortality compared to the opposite (Blanchfield & Ridgway 2005).

Another strategy females employ to potentially increase reproductive success is to spawn in multiple redds. Blanchfield and Ridgway (1997) reported that for two spawning

seasons females averaged 1.4 ± 0.8 and 1.7 ± 0.8 redds, with larger females constructing significantly more redds than smaller females in one of those seasons. As female fecundity is proportionally related to body length (Vladykov 1956), it would make sense that larger females construct more redds because they have more eggs to allocate. Additionally, brook trout are indeterminate growers, increasing in size throughout life. Combining this with the fact that many lotic brook trout populations have high juvenile growth rate and high adult mortality (Hutchings 1993, Morita & Morita 2002, Kennedy *et al.* 2003), older, and therefore larger, females might benefit from using a bet-hedging strategy such as multiple redd construction in an effort to reproduce with more males, potentially increasing reproductive success. Taggart *et al.* (2001) reported that over a period of three spawning seasons more than 50% of female Atlantic salmon were attributed to multiple redds genetically, and that those fish were significantly longer than ones attributed to a single redd.

Male Reproductive Strategies

Male reproductive success is primarily determined by mating opportunities. Hutchings and Gerber (2002) hypothesized that males have a higher mobility during the spawning season in an effort to increase reproductive success through increased encounter rates with females. For a lotic population, Hutchings and Gerber (2002) reported that males dispersed four times as far as females during the spawning season. They reported a tendency for smaller males to move further than larger males, but with removal of a single outlier this relationship became insignificant. Additionally, they

hypothesized that reduced movement by females reflected the competition for and retention of spawning ground. They reported no relationship between distances moved and body length for females.

These data suggest a mating system in which male brook trout move at high frequencies from female to female. Reasons for this may be to assess the size of the female (males prefer larger females (Blanchfield & Ridgway 1999)), and to assess the size and number of males present. For a lacustrine population, the number of males surrounding a spawning female ranged from one to nine with an average of three (Blanchfield & Ridgway 1999). Blanchfield and Ridgway (1999) reported peripheral males participated in 49% of all spawnings when less than four were present, and in 100% of all spawnings when five or more were present. Blanchfield et al (2003) reported that all 6 observed spawning events had peripheral male participation. Despite this, $92.3 \pm 11.9\%$ of a given brood were sired by the first male to spawn, usually the dominant male, and 52% (17/33) of all males made no genetic contribution (Blanchfield *et al.* 2003). Instead a few males spawned multiple times, with the number of broods a male was attributed to increasing significantly with body length.

An alternate hypothesis proposed to explain sex-biased movement is that it's a strategy employed to avoid breeding with closely related individuals (Greenwood 1980). Blanchfield et al. (2003) reported evidence refuting this hypothesis, suggesting that male brook trout did not seek out or avoid mates based on kinship. This subject is further confounded by evidence that salmonids are able to identify individuals sharing the same major histocompatibility gene through pheromones released into the water making kin

recognition possible (Nordeng & Bratland 2006). The extent to which relatedness determines mate choice is still unclear.

Mate Choice

Females directly influence their reproductive success through their choice of mate. Females select mates based on their physical traits and courtship displays (Barbosa & Magurran 2006). Male competition for access to spawning females is size-based (Blanchfield & Ridgway 1999, Blanchfield *et al.* 2003), resulting in a hierarchy with the dominant male being closest, and an outer ring of smaller peripheral males surrounding them. A male's size is relative, dependent on the size of the other males competing for access to the female (Gross 1996). Thus, even though a male may gain access to a female, that female may choose to delay spawning in an attempt to improve reproductive success (Foote 1989, Blanchfield & Ridgway 1999). This sets up the potential for size-assortative mating. Blanchfield and Ridgway (1999) reported that for a lacustrine population of brook trout, the size of the female explained 28% of the variation in the size of the dominant paired male. They also reported that females paired with a relatively smaller male took significantly longer to spawn than females paired with a male of equal or greater length. For the time period four to six hours before spawning to the onset of spawning, the length of the dominant male significantly increased. This suggests that males were actively moving around the spawning grounds.

Males of many salmonid species exhibit mating strategies involving relatively much smaller males darting into the spawning site and releasing milt as the female and dominant male are spawning (Gross 1985). This mating strategy has been termed "sneaking" because the smaller male does not compete with the larger male for access to

the female. It has evolved as a frequency dependent evolutionary stable strategy with males utilizing it contributing to a small percentage of fertilizations and, through heritability, ensuring its continued existence (Gross 1985). Furthermore, Gross (1985) stated that males of intermediate length were at the greatest disadvantage for spawning success in that they were too small to compete with larger males, and too large to use available habitat to hide and thus sneak fertilizations.

For resident brook trout populations, the presence of multiple cohorts mating simultaneously, along with length variation within a cohort, creates a wide range in lengths for mature males. Mature small males often do not display the typical morphological characteristics associated with being mature (personal observation), setting up the possibility of a mating strategy similar to that described by Gross (1985).

Population Structuring

Many salmonid species are reported to home to their natal incubation site to spawn with great precision (Dittman & Quinn 1996, Neville *et al.* 2006). Quinn *et al.* (1999) reported straying rates of 1% or less for anadromous populations of sockeye salmon (*Oncorhynchus nerka*). The mechanism utilized in homing has been hypothesized to be the initial imprinting of the odor of the natal incubation site, and a relocation of that site through olfactory detection of cues in the water. Stewart *et al.* (2004) provided direct evidence of this through displacement experiments involving spawning adult sockeye salmon and utilizing upstream and downstream sites. Displaced individuals were significantly more likely to return to their initial location when placed at the downstream location, and thus in the flow of olfactory cues from their natal site. However, Nordeng

and Bratland (2006) provide evidence refuting this hypothesis in favor of one where individuals relocate to a site by detection of pheromones released by related individuals. Regardless, homing behavior does occur for a variety of salmonids.

For lacustrine brook trout populations, the percentages present on the same spawning grounds in consecutive years has been reported as ranging from <1% to 8% (Vladykov 1942), to 9.7% (Baril & Magnan 2002), to 17% and 43% (Oconnor & Power 1973). Baril and Magnan (2002) report that their estimate may have been biased low due to heavy fishing pressure on the study population. For a lotic population, 4.1% of the population was captured at two spawning ground locations separated by approximately 1.5 km over a period of five years (Wilson *et al.* 2004). Combining this information with the bias for males to move greater distances than females during the spawning season (Hutchings & Gerber 2002) could allow for population structuring through female reproduction, with male movement supplying gene flow. If this is indeed what happens, then barriers inhibiting movement could have detrimental effects through loss of genetic diversity. Wofford (2005) reported that for coastal cutthroat trout (*Oncorhynchus clarki*) populations, gene diversity and allelic richness decreased as the number of barriers between sub-populations increased.

Pedigree Reconstruction

In light of brook trout reproductive tactics and ecology, the use of genetic techniques for inferring relationships between individuals is necessary. The majority of brook trout populations are open, allowing for immigration and emigration (Gowan & Fausch 1996, Carlson & Letcher 2003), spawn in relatively shallow water (0.4 m (Essington *et al.* 1998)), are polygamous (Blanchfield *et al.* 2003), and have no parental

care (Blanchfield *et al.* 2003). All of these factors make behavioral observations of spawning events difficult. Even if the spawning is observed and the putative parents are identified, with multiple milt release by males (Blanchfield & Ridgway 1997, Blanchfield *et al.* 2003) it is impossible to determine the proportion of eggs sired by each male.

Currently the best choice of genetic markers for inferring parent-offspring and sibling relationships are microsatellites (Wilson & Ferguson 2002). When used at multiple loci, their potential for high genetic diversity coupled with their codominant expression results in an increased exclusion probability for analyzing putative relationships (Wilson & Ferguson 2002). The use of microsatellite markers combined with parentage and sibship algorithms have been employed successfully in naturally reproducing salmonid populations (Taggart *et al.* 2001, Garant *et al.* 2001, Wilson *et al.* 2003a), and populations with some aspect of hatchery association (Letcher & King 2001, Fishback *et al.* 2002, Wilson *et al.* 2003b, Mclean *et al.* 2004, McDonald *et al.* 2004).

Summary

To date, no study has combined estimates of brook trout reproductive success with other aspects of individual life history. I propose to utilize mark-recapture techniques coupled with estimates of reproductive success based on pedigree reconstruction to determine how life history strategies involving growth and movement influence patterns in mate choice, survival and age at maturation and their resulting consequences for lifetime reproductive success in a lotic population of naturally reproducing brook trout (Figure 1). I propose to address the following questions for each chapter of my dissertation:

Proposed Questions

1) Does increased male breeding dispersal increase reproductive success?

Theoretical models examining the evolution of reproductive dispersal almost always include selective forces acting to increase the fitness of dispersing individuals (Hendry et al. 2004). One way an individual's fitness can be increased is through an increase in reproductive success. One strategy to accomplish this might be to increase breeding dispersal in an effort to find and potentially reproduce with more mates.

Salmonid populations have been reported as having male-biased breeding dispersal (Hutchings & Gerber 2002). This strategy is hypothesized to be an adaptation selected for through increased reproductive success (Hutchings & Gerber 2002). To date, empirical data supporting this hypothesis have not been collected.

2) In a polygamous mating system where males compete for females, what factors determine mate choice?

Mate choice directly influences the fitness of offspring. Mate selection is dependent upon the type of mating system present. Breeding system theory classifies mating systems based on level of parental care, spatial distribution of resources, and temporal distribution of mates (Emlen & Oring 1977). A polygamous mating system is predicted to occur when parental care is minimal, spatial resources are unevenly distributed and temporal distribution of mates is moderately asynchronous (Emlen & Oring 1977). Such a system would free up individuals from rearing young, while allowing one sex to monopolize resources and acquire mating rights to multiple individuals of the temporally asynchronous sex. The result would be an operational sex ratio skewed towards the

monopolizing sex. This leads to selection for intra-sexual competition and increased variance in reproductive success for that sex (Emlen & Oring 1977).

Salmonid mating systems are polygamous and display male-biased operational sex ratios (Maekawa *et al.* 1994, Blanchfield & Ridgway 1997). Males typically arrive at the breeding grounds first, require very little time out between reproductive efforts, and remain mature throughout the breeding season. Female reproductive activity is limited temporally by egg number and nest construction, and reproduction is asynchronous with larger females spawning first (Blanchfield & Ridgway 1997). Such conditions always favor increased numbers of reproductively active males over females, regardless of the underlying sex ratio. This results in increased selection for male-male competition, reinforced by reproductive success of competitively superior males.

Factors limiting reproductive success differ between males and females. Males are primarily limited by mating opportunities, and secondarily limited by mate quality. Females are primarily limited by resource competition. In salmonids, body size is typically indicative of competitive superiority in both sexes (Blanchfield *et al.* 2003, Blanchfield & Ridgway 2005). Therefore large males should be competing for mating access with large females due to higher fecundities and superior nest sites. But given the wide range in size for both sexes in mature brook trout, and the temporal asynchrony of female spawning, large males may attempt to mate with females of all sizes. Alternatively, mating pairs may be size selective with females mating with similar sized males. These two scenarios have vastly different implications for life history strategy employed by males, and for the resulting demographics.

3) **Do differing life history strategies result in equal lifetime reproductive success?**

Life history theory is based on trade-offs involving reproduction and survival. Nature should select for life history strategies optimizing reproductive success. Still, there exists individual variation in age at maturity and survival suggesting multiple optima resulting in the same fitness.

Theory states that optimization of lifetime reproductive success should be predicted by mortality rate and variation (Stearns 2000). Mortality rate predicts the optimum time and effort for reproduction. High mortality rate selects for individuals to mature early and increase reproductive effort early in life (Charlesworth 1980). For example, Trinidadian guppies adapted to habitat containing no predation pressure, shifted to life history tactics of earlier maturation, and production of more offspring in less than 50 generations when exposed to mortality from predators (Reznick 1990).

Variation in mortality rate results in variation in reproductive success, and thus variation in fitness. Variation in mortality often arises from variation in the environment caused by stochastic conditions (Saccheri & Hanski 2006). Life history theory predicts that organisms inhabiting risky environments should evolve traits to minimize variance in fitness (Stearns 2000). Adaptations for dealing with risk are referred to as “bet-hedging” strategies. One such strategy employed to spread the risk is to increase the number of independent reproduction events (Stearns 2000). This strategy involves both spatial (multiple reproductive efforts within a spawning season), and temporal (iteroparous) reproductive events. The extent to which environmental variation influences lifetime reproductive success is dependent on the lifespan and age-specific fecundities of the species, and has the greatest impact on short lived species (Clutton-Brock 1988).

Salmonid life history strategies are often dictated by thresholds achieved from growth rate and size (Hutchings & Jones 1998, Letcher & Gries 2003, Obedzinski & Letcher 2004). Individuals achieving a certain threshold mature at an earlier age, but may also be subject to greater mortality rates (Hutchings *et al.* 1999). Reproductive success may also be lower for early maturing individuals due to size constraints. Both female fecundity (Vladykov 1956) and male competitive ability (Blanchfield *et al.* 2003) are positively correlated with length. This leads to the question: Do individuals with different ages at maturity and survival rates experience similar lifetime reproductive success?

4) **Are life history strategies and reproductive success heritable traits?**

Individual reproductive success increases fitness only if resulting offspring also reproduce successfully. If life history traits are heritable, offspring success might in large part be determined by the parents. There has been debate over how much additive genetic variation should be associated with fitness traits (Merila & Sheldon 1999, Merila & Sheldon 2000), owing to the belief that such traits should be under high selective pressures and therefore exhibit low levels of variation. But recent data has shown that many fitness related traits exhibit relatively high heritability values (Burt 1995, Fowler *et al.* 1997). Hypotheses attributed as causes for this include balance of mutation-selection forces, (Barton & Turelli 1989), genotype x environment interactions (Turelli & Barton 2004), negative genetic correlations and pleiotropy (Turelli & Barton 2004), and differing fitness profiles for fitness components (Stearns 1992).

For species residing in stochastic environments, where variation in mortality can greatly influence individual lifetime reproductive success, there is selection for

individuals to mature and focus reproductive effort early in life (Charlesworth 1980). This suggests that faster growing individuals may have a fitness advantage through increased lifetime reproductive success in populations occupying stochastic environments where size conveys fitness.

For indeterminate growing organisms, growth rate and size at age predict many life history decisions (Metcalfe *et al.* 1988, Hutchings & Jones 1998, Letcher & Gries 2003, Obedzinski & Letcher 2004). Additionally, genetic variation in growth rate has been reported as having a significant heritable component in salmonids (Jonasson 1993, Garant *et al.* 2003). This implies that for salmonids, life history strategies may be heritable traits. If family life history strategies are successful, this would lead to disproportionately large contributions of that family to subsequent generations, decreasing the effective size of the population.

In the event of problems encountered leading to the inability to complete any of the above questions, I propose the following alternative question as a replacement.

5) Do sex differences in breeding dispersal patterns reflect predictions from theory?

In a review of sex differences in dispersal for birds and mammals, Greenwood (1980) concluded that patterns observed were dependent on the type of mating system utilized. Emlen and Oring (1977) defined monogamous mating systems as “Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness is often

maximized through shared parental care.”, and polygamous mating systems as “Individuals of one sex frequently control or gain access to multiple individuals of the other sex.” They further distinguished types of polygamous mating systems based on methods used to control or gain access to members of the opposite sex. These included indirect means through control of resources, direct means through control of individuals, and selection by the opposite sex based on intra-sexual competition.

The type of polygamous mating system employed is predicted to be determined by the distribution of resources and mates (Emlen & Oring 1977). If resources or members of the opposite sex are highly clumped, this allows for monopolization by competitively superior individuals. Alternatively, if resources or mates are widely dispersed, or if defense of them is intense, such as through high operational sex ratios, the cost of monopolization outweighs the benefits and a dominance hierarchy competing for mating access would be expected (Emlen & Oring 1977).

In dominance hierarchy polygamous mating systems, dispersal is higher for individuals of the limited sex (Greenwood 1980). One hypothesis for this is to increase reproductive success through increased encounter rates with potential mates (Greenwood 1980, Hutchings & Gerber 2002). This would be a logical adaptation to systems where mates are widely dispersed. Another hypothesis is to avoid areas with closely related kin (Greenwood 1980). Such a strategy would reduce inbreeding depression, but may also improve mating opportunities if behavior biasing mate choice is influenced by kin-recognizing abilities.

Salmonid mating systems are polygamous, with an operational sex ratio skewed towards males (Blanchfield *et al.* 2003), creating intense male-male competition for

access to females. Additionally, spawning grounds can be widely dispersed, especially for lotic populations constrained by a linear network of streams. Given these characteristics, breeding theory predicts that dispersal should be occurring for the limited sex, in this case males, during the breeding season.

Study Site

The study site will be an approximately kilometer long reach of the West Brook, a third order tributary of the Mill River located in Whately, Massachusetts, and the initial 280-300 meters of three second order tributaries whose confluences enter within this study reach. The value of 280-300 meters is not arbitrary, but instead is based on locations of natural barriers, two of which are impassable by trout. The streams contain naturally reproducing populations of brook and brown trout, and a population of Atlantic salmon that is stocked in as fry (Letcher & Gries 2003).

Sampling Methods

Sampling has been ongoing in the main stem of the West Brook since 1997. Sampling occurs seasonally and the protocol consists of dividing the study reach into approximately 20 meter sections and setting up block nets at the upstream and downstream ends of the section. Two-pass removal using electrofishing techniques is then performed (for further details see (Letcher *et al.* 2002)). I propose to continue sampling the main stem in the same fashion, and to add the sampling of the three tributaries but with the following changes: only use one-pass removal, and do not use any

block nets because of their smaller size. I propose to undertake this sampling for a period of three years in an effort to follow multiple cohorts.

On their initial capture, all individuals at least 60 mm in length and 2.0 g in mass will be implanted with a passive integrated transponder (PIT) tag (12-mm Digital Angel Corp., St. Paul, MN) providing a means to uniquely identify individuals upon subsequent recapture. Also on its initial capture, a portion of the individual's anal fin will be removed and stored in ethanol for genetic analyses, and scales will be taken if the fish cannot be assigned to a year class in the field. Additional variables recorded upon capture will be length (± 1 mm) and mass (± 0.01 g) of the individual, its location of capture, and its sex and maturity status if identifiable.

To supplement seasonal electrofishing for determining individual's positions and movements, I propose using a combination of stationary PIT tag antennas and a portable PIT tag wand technique. Two stationary antennas were installed in the fall of 2001 and are located downstream of the main stem (Zydlewski *et al.* 2006). An additional antenna will be installed upstream of the main stem reach, and one at each confluence of a tributary with the main stem. Stationary antennas offer the advantage of continuous monitoring, with the drawback of only sampling a fixed point. In an attempt to partially remedy for this I propose using a portable PIT tag antenna wand technique which would involve a complete surveying of the study sections of each tributary at monthly intervals (Zydlewski *et al.* 2001, Hill *et al.* 2006). Data recorded for a detected individual would include location (nearest quarter of a section), habitat (run, riffle, or pool), and time and date.

Genetic Methods

Total genomic DNA will be extracted from the anal fin clips using a cell lysis method. Extractions will be performed for all individuals ever having been detected in a tributary, and a subset of individuals from the West Brook population that were known to be mature or were greater than 140 mm. Each individual will be genotyped at twelve loci using primers developed for brook trout (Tim King, USGS, Leetown Science Center, Kearneysville, WV, unpublished data) and Atlantic salmon (King *et al.* 2005). If need arises additional loci can be added. The forward primer for each loci will be labeled with a fluorescent marker (FAM, HEX, or NED (Applied Biosystems, Foster City, CA)), and DNA will be amplified using a polymerase chain reaction (PCR) with specifications obtained from the King laboratory on an MJ Research DNA Engine Dyad Thermocycler (Waltham, MA). PCR product will be analyzed using a Hitachi ABI 3100-Avant Genetic Analyzer (Applied Biosystems) in multiplexed groups of four loci based on allele size and fluorescent label, and run with a ROX-labeled size standard (Applied Biosystems). Fragment sizes will be analyzed using Genescan software (Applied Biosystems), and genotypes will be generated by hand calling of alleles in order to reduce error. All genotypes will be imported into a database and referenced to an individual through its PIT tag identification number.

Pedigree Reconstruction

I propose using a combination of both sibship and parentage assignment techniques obtained from multiple software programs in order to assess their congruence of pedigrees. A sampling of the software programs I intend to use for parentage

assignment include: PASOS (Duchesne *et al.* 2005), CERVUS (Marshall *et al.* 1998), PARENTE (Cercueil *et al.* 2002), FaMoz (Gerber *et al.* 2000), and PedAPP (Almudevar 2007). Software programs for sibship reconstruction include: PEDIGREE (Smith *et al.* 2001, Butler *et al.* 2004), COLONY (Wang 2004), KINGROUP (Konovalov *et al.* 2004), and PRT (Almudevar & Field 1999).

To estimate genotyping error I propose randomly selecting one hundred individuals for which new DNA extractions and genotyping will be performed. The two genotypes will then be compared for each individual, and a population error rate will be estimated based on the number of differing genotypes. To assess the influence of genotype errors on pedigree output, reconstructions can be performed on a simulated pedigree (Anderson & Dunham 2005) with varying rates of genotype error introduced into it, including the estimated error rate from the empirical data. Departures from known data can then be calculated and interpreted. The finalized pedigree will be used for all analyses involving reproductive allocation and relatedness.

Analyses

- A. Generate pedigrees for each of the tributary populations using all fish observed in a tributary, and a subset of fish from the West Brook consisting of mature and large (> 140 mm) individuals. Initial analyses indicate that pedigree reconstruction is possible. Using program PASOS, the proportion of individuals having parents allocated to them were 0.69, 0.85, 0.88, and 0.92 for the 2002 through 2005 cohorts respectively. Exclusion probabilities from the twelve loci

are 0.977 for the first parent and 0.999 for the second parent, suggesting a high confidence in assignments that will be verified through simulations.

B. Numbers represent respective dissertation chapters.

1. Calculate movement metrics for mature males during the spawning season. Metrics could include total movement, frequency of movement, and average distance moved using all methods of individual detection. Regress the number of females a male is attributed to have spawned with against the above movement metrics and determine proportion of variance explained.
2. Acquire sizes of males and females for attributed matings. In cases where females are attributed to multiple males, determine dominant male through male sizes or number of attributed offspring. Regress size of dominant male on size of female and determine proportion of variance explained.
3. Group individuals by life history strategy based on sex and age at maturation determined from the pedigree. Calculate the lifetime reproductive success of individuals in differing life history groups. Use separate analysis of variance tests to determine differences among life history groups for each sex. Employ optimality modeling (Mangel & Clark 1988, Parker & Smith 1990) to compare actual versus maximal lifetime reproductive success strategies.
4. Determine reproductive success of parents and offspring from pedigree. Calculate survival using Cormack-Jolly-Seber models in program Mark (White & Burnham 1999). Calculate individual growth rates in weight

(Ostrovsky 1995) and length using consecutive electroshocking capture events. Determine individual age at maturity from pedigree. Calculate heritability values for growth rate, survival, and age at maturity using the animal model (Falconer 1981, Kruuk 2004, Garant & Kruuk 2005).

5. Calculate movement metrics for mature males and females during the spawning and non-spawning seasons. Metrics could include total movement, frequency of movement, and average distance moved utilizing all methods of individual detection. Compare seasonal metrics for each sex using a non-parametric differentiation test such as a Kolmogorov-Smirnov test.

- 6.

Time Line

Data Generation

Conduct the three phases of the field sampling (electrofishing, PIT Tag wanding, and PIT Tag Antenna monitoring) from June 2002 through June 2005.

Complete the genotyping component for the initial 12 loci for all individuals captured in the tributaries belonging to the 2005 cohort or earlier, and selected large or mature individuals captured in the West Brook by March of 2007. In the event of the need for additional loci, I would allow for another two months for up to four loci.

Data Analysis and Writing

Conduct pedigree reconstruction simulations to evaluate algorithm efficiencies.

Construct final pedigree for analysis using best algorithm: Project to finish by June, 2007

Hypothesis/Chapter 1: Analysis awaiting final pedigree reconstruction, project to finish writing by August, 2007

Hypothesis/Chapter 2: Analysis awaiting final pedigree reconstruction, project to finish writing by October, 2007

Hypothesis/Chapter 3: Analysis awaiting final pedigree reconstruction, project to finish writing by December, 2007

Hypothesis/Chapter 4: Analysis awaiting final pedigree reconstruction, project to finish writing by February, 2007

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