A LIFE HISTORY APPROACH TO UNDERSTANDING MARINE EXIT TIMING OF A SOCKEYE SALMON POPULATION FROM HAIDA GWAII

By

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ABSTRACT

This thesis examines the individual variation of marine exit strategies within a population of sockeye salmon known to have early marine exit timing and long delays before spawning. Mean delay was 134 days and represents some the longest known wait times of any sockeye salmon population. Thermal limit avoidance hypotheses were not able to explain this behaviour, as the thermal regime of the stream was moderate. Marine exit date was not correlated to spawning date, as fish were able to spawn at any time (early or late) regardless of their marine exit strategy. Individuals with early marine exit strategies had higher growth, greater somatic energy density, smaller gonads, and greater fecundity. In addition, males and older fish migrated earlier than females and younger fish. These data are explained using a simple life history model and support the hypothesis that marine exit timing is a condition-dependent life history decision.

KEYWORDS: salmon, migration, river entry, marine exit, migration strategy, condition-dependent migration, life history strategy.

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Finally to Jenna

Thank You

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

1.1 Background

Anadromous species such as sockeye salmon (*Oncorhynchus nerka*), which form the subject of this thesis, migrate to sea to take advantage of the relatively productive marine environment (compared to freshwater environments). Fish species with this life history strategy gain fitness benefits from the increased growth available at sea that outweigh the costs of increased mortality and energetically costly migrations (Bernatchez and Dodson 1987, Gross 1987). The usual pattern is for juvenile fish to migrate to the open ocean where they take advantage of good growing conditions. Upon maturing as adults they return to their natal river system through which they migrate to spawning areas, arriving a few days or weeks before spawning begins in the fall. This thesis focuses on 'marine exit', the time at which individuals depart the productive marine environment and enter freshwater rivers to commence migration to spawning areas.[1]

The timing of marine exit, river migration, and spawning are thought to be a population-specific adaptation to local environmental conditions (Groot and Margolis 1991, Taylor 1991) that affect the probability of successful spawning (Young et al. 2006) and emergence of offspring the following spring (Brannon

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[1] While landlocked sockeye salmon (kokanee) do not migrate to sea, they migrate into lakes, which have higher productivity than their natal streams. Marine exit strategies used by anadromous populations are therefore analogous to exit strategies of kokanee as they migrate from lake feeding areas to tributary streams to spawn.

1987; Webb and McLay 1996). Variation of individual marine exit timing within a population has been considered a non-adaptive by-product of the fish's distribution at sea at the moment homeward migration is initiated, such that individuals closer to their natal stream arrive earlier than those further away (Gilhousen 1960, Hodgson et al. 2006). However, recent work has shown that body condition parameters, such as energetic and reproductive state, are important drivers of marine exit timing of some Fraser sockeye salmon populations (Cooke et al. 2008a, Cooke et al. 2006a, Cooke et al. 2006b, Cooke et al. 2008b, Crossin et al. 2007, Crossin et al. 2008, Crossin et al. 2009, Hanson et al. 2008, Young et al. 2006). This suggests that the variation of individual marine exit timing within a population may result from variation in the conditions experienced while at sea.

The variation of median marine exit timing among different populations appears to be an adaptive balance between optimal spawning date and maximizing the probability of successful migration to spawning areas (Quinn 2005a). Hodgson and Quinn (2002) proposed three thermal migration timing strategies to explain the variation in marine exit timing observed among sockeye populations. These are as follows: (1) If the thermal regime during incubation dictates early spawning, then fish return early, before summer temperatures peak, and spawn with little delay. This strategy was proposed for interior sockeye populations that experience long energetically costly migrations and cold winters during egg incubation. (2) If the thermal regime during incubation is mild, dictating late spawning, then fish may return late in the season, after temperatures peak, and spawn with little delay. This strategy was proposed for coastal sockeye populations with short, easy migrations (< 100 km) and mild winters during egg incubation. (3) If the thermal regime during incubation is mild, dictating late spawning, but the river thermal regime prior to spawning is warm, populations may migrate to fresh water early (before temperatures peak) and experience a long delay in the lake before spawning. This strategy was proposed for coastal sockeye populations with short, easy migrations (< 100 km) at the southern end of the range that experience high peak average river temperatures (≥19°C).

Sockeye salmon populations returning to streams on the islands of Haida Gwaii, off the coast of northern British Columbia, exhibit a wide range of marine exit timing within and among populations, even though all spawn at similar times over a relatively short duration (Figure 1.1). Marine exit timing of these populations can be separated into groups with early and with late marine exit. Phylogenetic comparisons indicate that early marine exit behaviour has evolved independently in a number of river systems on Haida Gwaii and elsewhere (Beacham et al. 2006). As will be shown, individuals from early marine exit populations can experience freshwater residence periods as long as 160 days prior to spawning. This phenomenon is especially interesting considering that fish from these populations leave the marine environment just as primary production and zooplankton in the North Pacific is peaking (Brodeur et al. 1996, Rand 2002; see Figure 1.1). Adult sockeye indirectly benefit from the seasonal

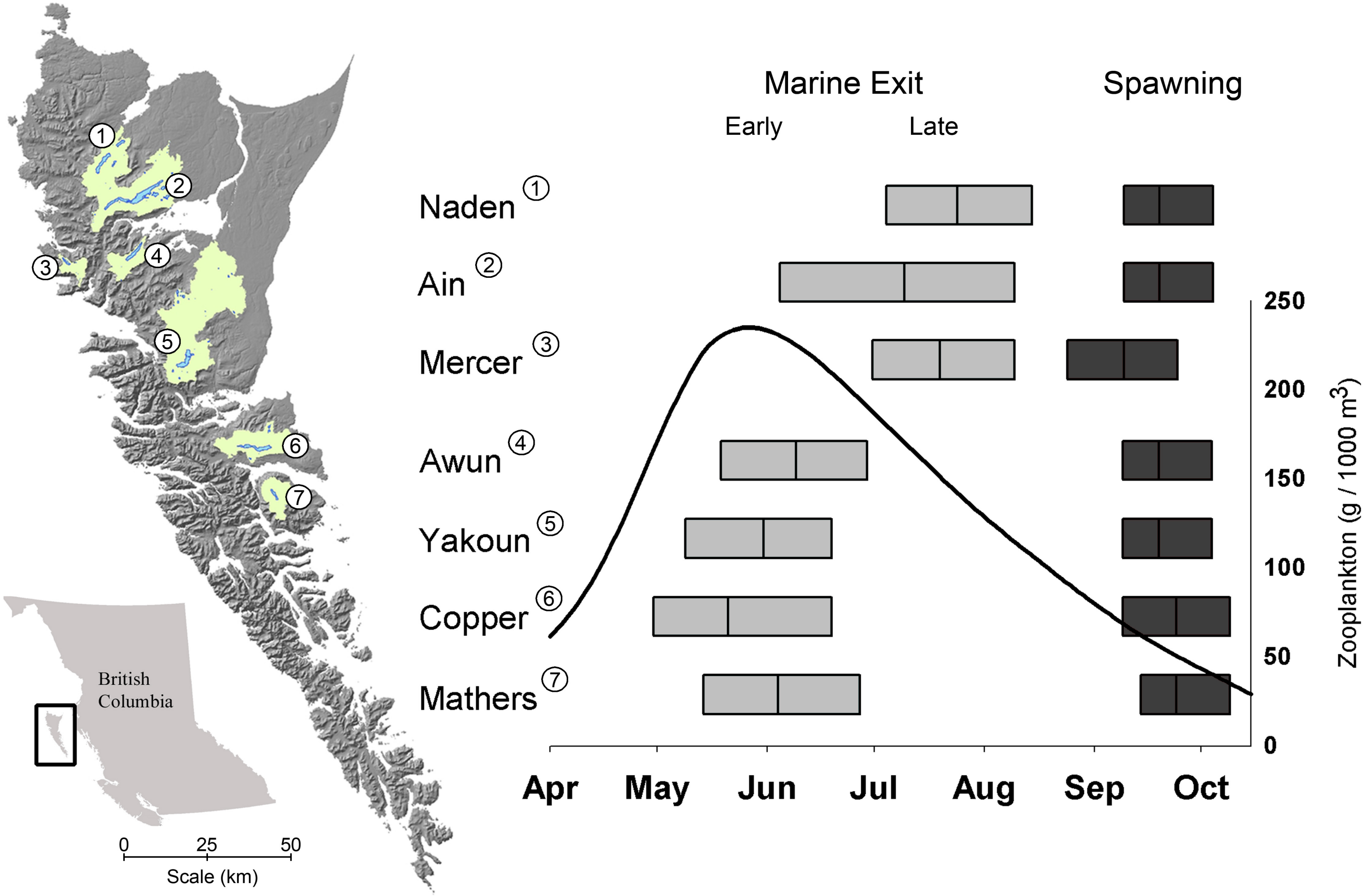

Figure 1.1 Locations of watersheds containing sockeye salmon populations on Haida Gwaii. Marine exit (light bars) and spawning (dark bars) timing is visually depicted for each population (unpublished data from Haida Fisheries Program). The curved line represents mean zooplankton density (right axis) in the Alaskan Gyre of the open Pacific Ocean as reported by Brodeur (1996). Zooplankton density is used as a surrogate of prey availability. Sockeye salmon indirectly benefit from the seasonal peak in primary production by feeding on organisms (e.g. euphausiids) that prey directly on the seasonal abundance of plankton.

peak in primary production by feeding on organisms (e.g. euphausiids) that prey directly on the seasonal abundance of plankton. The density of zooplankton can therefore act as a surrogate of food availability for adult sockeye salmon in the Pacific Ocean.

Because maximizing growth and energy reserves prior to spawning has direct benefits to reproductive potential (Gross 1985, Vandenberghe and Gross 1984), salmon should stay at sea to feed as long as possible prior to homeward migration and subsequent spawning. Therefore, a migration strategy consisting of early marine exit and long freshwater wait times prior to spawning should be considered to be energetically costly compared to later migration strategies. Hodgson and Quinn (2002) hypothesized that early migrating salmon populations that forego good growing conditions at sea are “making the best of a bad situation” by strategically avoiding higher water temperatures during the middle of summer (strategy iii from above). As the metabolism of salmonids is positively and non-linearly correlated with temperature (Fry 1971), the energetic cost of upstream river migrations increases dramatically at temperatures over 19°C. This strategy assumes that the increased cost of early migration is offset by reduced energy required to migrate upriver early in the season when river temperatures are lower.

In this thesis, marine exit date is viewed in fitness-maximizing terms, namely as an evolved life history decision influenced by: (a) marine growth opportunities, (b) mortality costs in the ocean in the period prior to marine exit, and (c) by the fitness costs of migration. The basic concept is analogous to that used in ‘age at maturity’ models (Stearns 1992). In the simplest such model, an organism grows until ‘maturity’, whereupon it ceases growth and reproduces. Expected reproductive success is a function of the size attained. Mortality occurs at a certain rate during the growth period, and may (but need not) be size dependent. The age at maturity that maximizes fitness is that at which the marginal fitness gains of further growth are equal and opposite to the marginal fitness cost of mortality. Analogously, marine exit is predicted to occur when the marginal fitness benefits and costs of prolonging ocean residence are equal. Fitness benefits of remaining at sea are derived from growth and accumulation of energy reserves. Specifically the improved spawning success from increased fecundity, egg size and competition for nest sites among females as well as improved competition and mate pairing among males that is largely attributed to body size and energy reserves. These benefits are compared to the mortality costs experienced at sea and during up-river migration.

1.2 Objectives and Outline

The general objective of this thesis was to gain a better understanding of how life history decisions influence the marine exit timing of sockeye salmon. More specifically the purpose was to: (1) determine if Hodgson and Quinn’s (2002) thermal avoidance hypothesis (strategy 3) is sufficient to explain the early marine exit timing and long freshwater waiting periods observed in sockeye salmon returning to a stream on Haida Gwaii, and (2) determine how physical condition dependence influences the marine exit timing strategies of individuals within a single population. My findings led me to propose an alterative hypothesis to explain the early marine exit timing of Haida Gwaii sockeye salmon populations based on a life history model.

More specifically, Chapter 2 documents the marine exit and subsequent spawning of sockeye salmon returning to Copper Creek, to characterize the long fresh water wait time known for this population along with the thermal regime of the stream during migration. The characteristics of this population were then contrasted to Hodgson and Quinn's (2002) hypothesised marine exit timing strategies to determine if they were sufficient to explain the observed marine exit timing of sockeye salmon returning to Copper Creek.

In Chapter 3, multiple measures of body condition were correlated with marine exit timing within a sockeye salmon population with early marine exit timing. More specifically, I predicted that older, larger, fast-growing individuals with high energy reserves would choose an earlier marine exit strategy, as the marginal benefits from remaining at sea would be less than those for their younger, smaller, slow-growing cohorts with low energy reserves.

Lastly (Chapter 4), I drew general conclusions from the results in Chapters 2 and 3 and discussed how a life history model can be used to explain the variation in marine exit timing observed within populations of salmon. I then proposed an alternative hypothesis, to Hodgson and Quinn's (2002) hypothesised marine exit strategies, to explain the early marine exit timing and long freshwater wait times observed in sockeye salmon returning to small coastal streams.

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CHAPTER 2: EARLY MARINE EXIT STRATEGY OF COPPER CREEK SOCKEYE SALMON (*ONCORHYNCHUS NERKA*)

2.1 Abstract

I examined the marine exit (river entry) and spawn timing of sockeye salmon returning to Copper Creek, a population known to have long freshwater wait times before spawning. This population leaves the marine environment and migrates upriver to its natal lake during May and June and then spawns in late September to early October. Mean delay between marine exit and spawning was 134 days and represents some of the longest known freshwater wait times of any sockeye salmon population. Marine exit date did not correlate to date of spawning. The stream's thermal regime was moderate (< 14^{o}C) during upriver migration and mid summer maximal stream temperatures, typically not exceeding 17.5^{o}C. Thermal limit avoidance hypotheses were unable to explain the early marine exit timing and long freshwater wait times prior to spawning in this population. A basic life history approach suggests that an alternative "cost" to upriver migration may be driving the trade-off associated with the early marine exit timing and long freshwater wait times prior to spawning in this population.

2.2 Introduction

Sockeye salmon (*Oncorhynchus nerka*), like other anadromous fishes, migrate to sea to take advantage of a more productive environment compared to the freshwater environments where they reproduce. Fish species with this life history strategy gain enough fitness benefits from the increased growth available at sea to outweigh the costs of increased mortality caused by these energetically costly migrations (Bernatchez and Dodson 1987, Gross 1987). As marine productivity and food availability in the North Pacific vary temporally (Brodeur et al. 1996), natural selection likely acts on migration timing, a highly heritable trait (Hansen and Jonsson 1991, Quinn et al. 2000, Smoker et al. 1998), to optimize these tradeoffs.

Population specific variation of migration and spawn timing are therefore assumed to be adaptations to local conditions (Groot and Margolis 1991, Taylor 1991). The main hypothesis used to explain spawn timing predicts that timing is such that the probability of successful spawning and survival of embryos during incubation is maximized, as well as growth and survival of offspring, after emergence the following spring (Brannon 1987, Webb and McLay 1996). Considering the strong relationship between salmon development and temperature, spawn timing is thought to be influenced mainly by the thermal regime during incubation (Quinn 2005). The timing of river entry, or as refer to here, ‘marine exit’, is therefore considered to be an evolved behavioural strategy that maximizes the probability of successful migration to spawning areas so that salmon can spawn at the time that maximizes their reproductive success (Hodgson and Quinn 2002, Hodgson et al. 2006).

Because maximizing energetic intake often leads to greater reproductive success in capital breeders such as salmon (Gross 1985, Healey et al. 2003, van den Berghe and Gross 1984), longer non-feeding delays between marine exit and spawning are not considered favourable due to forgone marine feed opportunities and the metabolic cost of holding in freshwater (Gilhousen 1960). In theory, salmon could maximize their reproductive potential by feeding at sea during the summer and return to their natal stream shortly before spawning. However, the delay between upstream migration and spawning varies considerably between populations and species of anadromous salmonids. Some populations migrate into their natal rivers in an advanced reproductive state and spawn soon after arrival, while others migrate into their natal stream in a less advanced reproductive state many months prior to spawning. The waiting period between migration and spawning is especially variable in populations of chinook salmon (Healey 1991), steelhead salmon (Busby et al. 1996), and sockeye salmon (Quinn et al. 1997).

Early migrating salmon populations that forego good growing conditions at sea are hypothesized to be making “the best of a bad situation” (Hodgson and Quinn 2002). High water temperatures experienced during upriver migration are often reported to increase mortality of sockeye salmon en route to spawning areas (Crossin et al. 2008, Keefer et al. 2008, Naughton et al. 2005, Patterson et al. 2007). The metabolism of salmonids is positively correlated with temperature

(Fry 1971, Lee et al. 2003). Therefore, higher temperatures experienced during migration result in higher energetic costs. Hodgson and Quinn (2002) proposed three migration timing strategies to explain the observed variation in marine exit timing among populations. Firstly (strategy 1), if the thermal regime during incubation dictates early spawning, then the fish exit early, before summer temperatures peak, and spawn with little delay. This strategy was proposed for interior sockeye salmon populations that experienced long energetically costly migrations and cold winters during egg incubation. Secondly (strategy 2), if the thermal regime during incubation is mild, dictating late spawning, then the fish may exit late in the season, after temperatures peak, and spawn with little delay. This strategy was proposed for coastal sockeye salmon populations with short easy migrations (< 100 km) and mild winters during egg incubation. Thirdly (strategy 3), if the thermal regime during incubation is mild, dictating late spawning, and the river thermal regime prior to spawn is warm; populations may exit early (before temperatures peak) and experience a long delay in the lake before spawning. This strategy was proposed for southern coastal sockeye salmon populations with short and easy migrations (< 100 km) that experience high peak average river temperatures (≥19°C).

This chapter examines a sockeye salmon population known to have early marine exit timing and long delays between upriver migration and spawning. The delay before spawning, referred to as “residence time” in this study, is defined as the period that an adult sockeye salmon spends in freshwater between the day it exits the marine environment and the last day it is observed during spawning. The timing of marine exit (river entry) and spawning was documented to characterize residence times at the individual and population levels. In populations with short residence times, such as those with migration timing strategies 1 and 2 proposed by Hodgson and Quinn (2002; see above), the timing of marine exit and spawning are strategically associated. This occurs because spawning strategies are directly affected by marine exit timing (Morbey 2000, Morbey and Ydenberg 2003). In contrast, marine exit and spawn timing are likely strategically independent in populations with long residence times, such as those with migration timing strategy 3 proposed by Hodgson and Quinn (2002). The reason is that all individuals have migrated into their natal lake and wait together prior to spawning. During this lake holding period, individual sockeye salmon are capable of behaviourally thermo-regulating (Newell and Quinn 2005), and likely have some degree of control over their reproductive development. I therefore predicted that the timing of spawning would not be correlated to marine exit timing because all spawn-timing options would be available to all individuals, regardless of marine exit timing. As such, individuals that exit the marine environment early will on average have longer residence times than their later migrating cohorts.

Secondly, the stream's thermal regime encountered by fish during migration was measured to determine if marine exit strategy 3, proposed by Hodgson and Quinn (2002) is sufficient in explaining the early marine exit timing observed in this population. This strategy specifically refers to coastal sockeye salmon populations at the southern end of the species range that experience high peak average river temperatures (≥19°C). Sockeye salmon returning to northern coastal British Columbia typically experience ambient air and water temperatures that are much cooler compared to southern populations. I therefore predicted that the thermal regime of Copper Creek, would be cool (< 19^{o}C) during migration and therefore Hodgson and Quinn's migration timing strategies would be insufficient to explain the early marine exit timing and long residence time of sockeye salmon returning to Copper Creek.

2.3 Methods

2.3.1 Study System

Copper Creek is a coastal watershed located on Moresby Island (Figure 2.1), an island within the archipelago of Haida Gwaii, off the coast of northern British Columbia, Canada. The watershed has a drainage area of 157.7 km^2 and drains northern Moresby Island eastward into Hecate Straight at Copper Bay (N 53^{o} 9' 45.31", W 131^{o} 48' 1.09"). This watershed is located on the Skidegate Plateau landform within the Coastal western hemlock, wet hypermaritime biogeoclimatic sub-zone (Figure 2.2). Skidegate Lake, the natal lake for Copper Creek sockeye salmon, has a surface area of 7.1 km^2 and drains 59% of the total watershed area. The mainstem of Copper Creek has a length of 13.1 km and elevation gain of 41 m from the estuary at Copper Bay to Skidegate Lake. The riparian forest is dominated by second growth Sitka spruce (*Picea Sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and red alder (*Alnus rubra*).

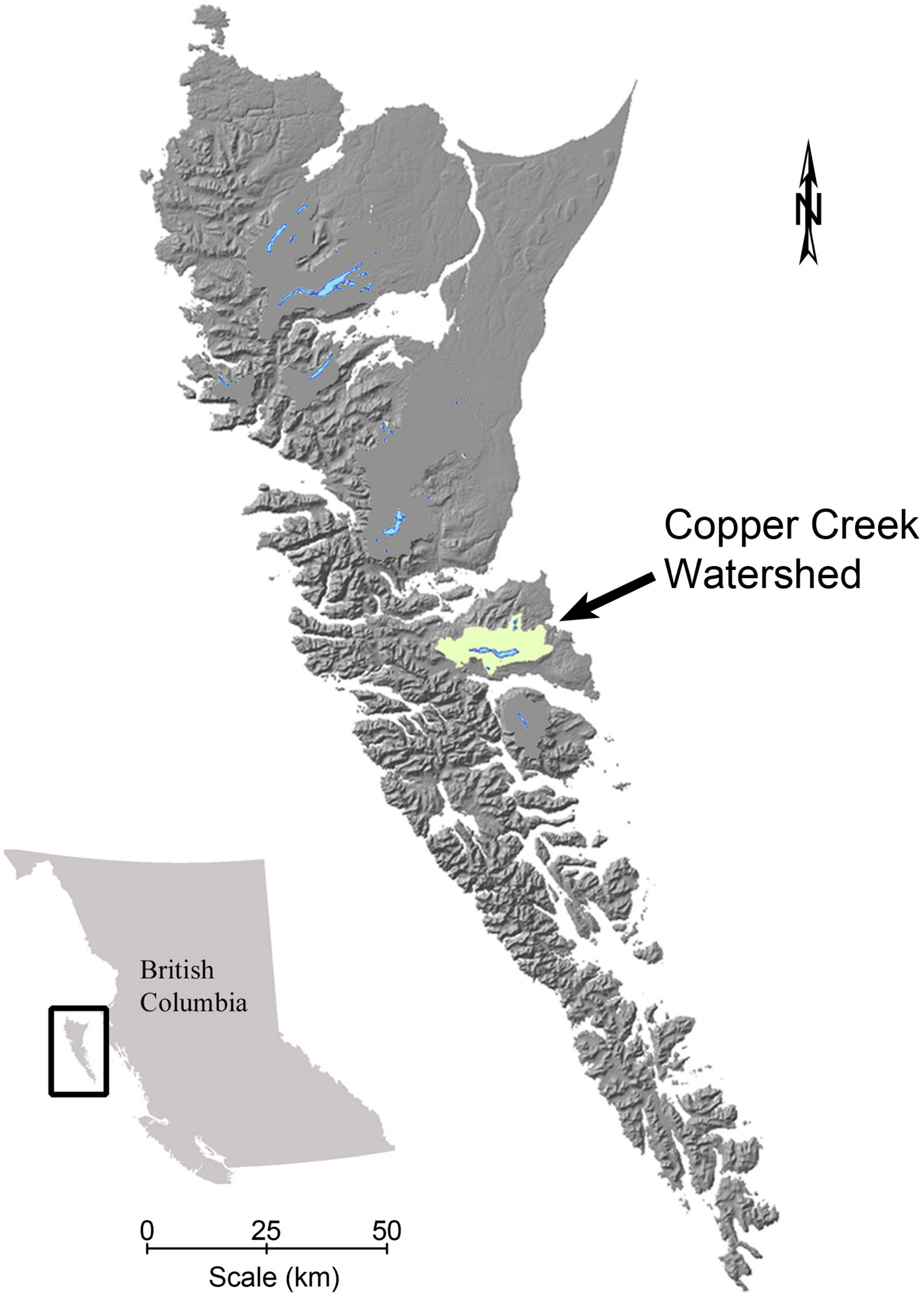

Figure 2.1 Location of the Copper Creek watershed on the islands of Haida Gwaii, British Columbia, Canada.

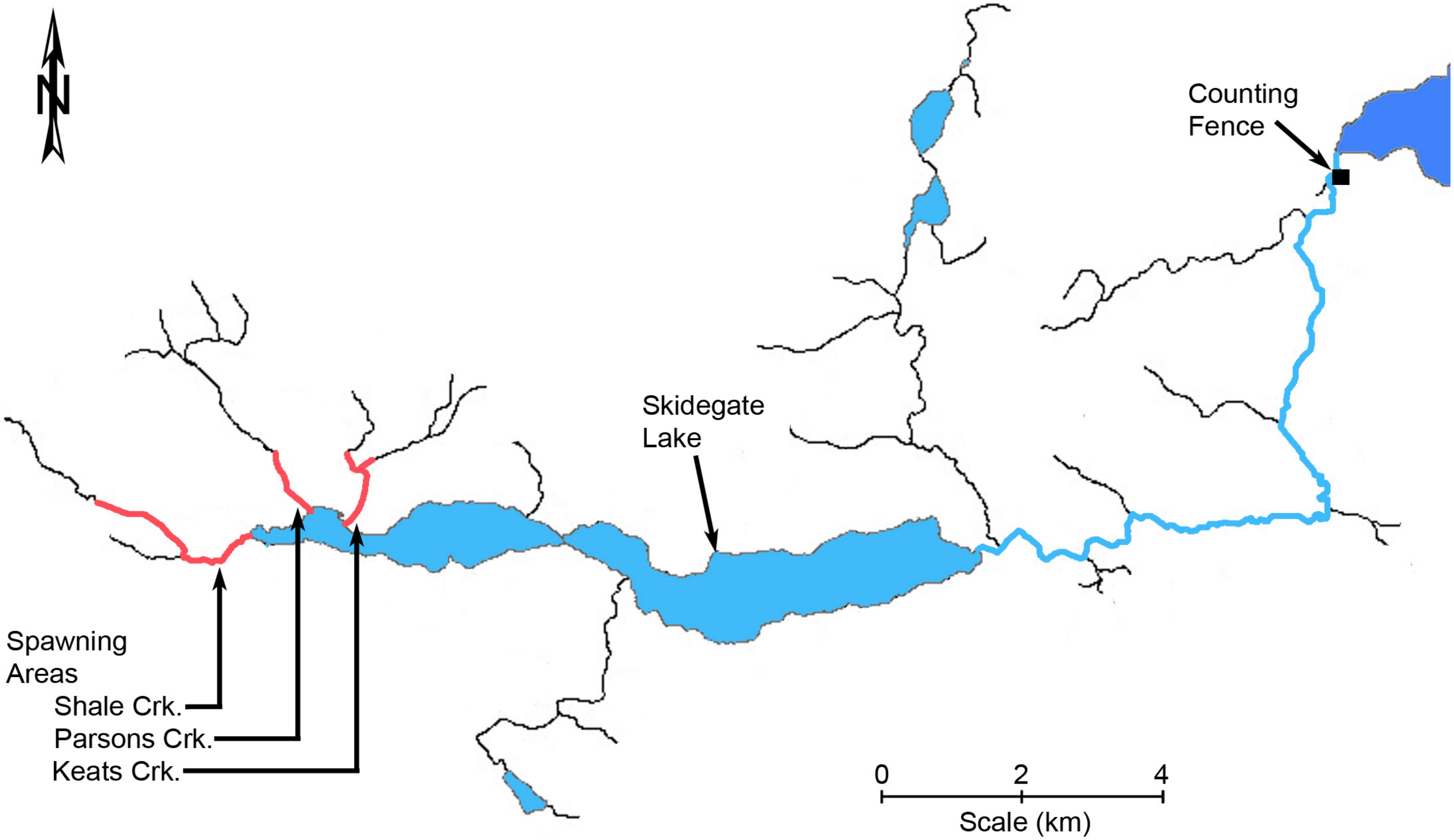

Figure 2.2 Location of study sites within the Copper Creek watershed.

Fish species within this system include pink salmon(*O. gorbuscha*), sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), steelhead salmon (*O. mykiss*), cutthroat trout (*O. clarki*), Dolly Varden char (*Salvelinus malma*), coast range sculpin (*Cottus aleuticus*), prickly sculpin (*C. asper*), threespine stickleback (*Gasterosteus aculeatus*), Pacific lamprey (*Lampetra tridentata*) and western brook lamprey (*L. richardsoni*). Adult sockeye salmon migrate up the mainstem of Copper Creek to Skidegate Lake in the spring and then hold in the lake during the summer months prior to spawning in the lake tributaries during the fall. Upon emerging from spawning gravels, juvenile sockeye salmon migrate downstream to Skidegate Lake where they rear in freshwater for 1-2 years prior to migrating to sea. Pink and chum salmon utilize the mainstem below the lake where coho salmon, steelhead and cutthroat trout are distributed throughout the watershed including the Skidegate Lake and its tributaries.

2.3.2 Marine Exit Timing

The Haida Nation has enumerated Copper Creek sockeye salmon since the early 1980's to assist the management of the Haida aboriginal food, social, and ceremonial (FSC) sockeye salmon fishery. From 1983 to 1993, sockeye salmon were enumerated by members of the Skidegate Band through the Community Economic Development Program sponsored by the Department of Fisheries and Oceans. Migrating fish were observed from a tower between the hours of 22:00 and 06:00, as they swam past a river-wide aluminium counting plate illuminated by gas-powered lights located approximately 2 km upstream from the mouth. In 1994, the Haida Fisheries Program constructed a floating fish weir at the mouth of Copper Creek located at 53^{o} 9’ 29.98” N, 131^{o} 47’ 59.89” W, and has used it to enumerate migrating Copper sockeye salmon to the present. The weir is composed of 16’ X 2’ floating aluminium panels that attach to hooks mounted on a wooden sill along the streambed and a “V” lead fish trap that was incorporated into the left embankment. Historical data consist of a combination of complete and partial counts using these two systems to estimate total escapement, along with reported catch from the Haida FSC fishery at Copper Bay.

The Copper Creek fish fence was operated between April 25 and July 1, 2005, and between April 23 and June 29, 2006. Fish were enumerated and released upstream of the fence using two methods. During periods of low migration rates, fish were captured in the “V” lead trap overnight and then enumerated as they were released upstream the following morning. During periods of high passage rates, Haida Fisheries technicians visually counted fish as they passed through two opened fence panels and over an aluminium counting plate illuminated by overhead electric lights between the hours of 22:00 and 06:00. Weather observations, stream and air temperature, and stream height from a permanent staff gauge were taken at the beginning of each shift of fish enumeration.

2.3.3 Spawn Timing and Residence Time

Adult sockeye salmon were collected from the trap at the Copper Creek fence for sampling and marking to estimate residence time and to test the correlation of marine exit and spawn timing. Fish were removed from the trap using a cradle net and placed into a foam-covered trough containing water pumped directly from the stream. Sampling included identification of sex, fork length measurement (±0.5 cm), and collection of two scales for age analysis. Acetate impressions were made of scales using a hydraulic press and interpreted by Birkenhead Scale Analysis (Lone Bute, BC) to determine ages of fish sampled (Clutter and Whitesel 1956, Gamble and Cox-Rogers 1993). Fish age is reported as suggested by Koo (1962), which identifies years spent in freshwater and the ocean. For example, an age reported as 1.2 refers to a fish that has spent one year in freshwater (fry to smolt) and two years at sea (smolt to adult). Coloured external marks supplied by Floy Tag Inc. (Seattle, Washington) were applied at the anterior base of the dorsal fin to identify the date of marking (i.e. arrival at the Copper Creek fish fence). In 2005, a total of 317 sockeye salmon were marked with uniquely numbered Petersen disks blocked into three colour groups identifying the early, mid, and late marine exit periods. In 2006, a total of 441 sockeye salmon were marked with two numbered Floy T-Bar Anchor Tags blocked into 12 separate five-day marine exit groups identifiable by tag colours. Upon completion of sampling and marking, fish were released into a pool upstream of the Copper Creek fence.

Copper Creek sockeye salmon spawners were observed in three tributaries at the western end of Skidegate Lake during the fall of 2005 and 2006. Sockeye salmon spawning habitat within Shale, Parsons and Keats Creeks extends from Skidegate Lake upstream to approximately 2100 m, 1300 m and

1100 m respectively. Observers walked along the stream bank of each tributary from the mouth at Skidegate Lake upstream to the end of spawning habitat. Spawning sockeye salmon were visually enumerated and external colour marks identified at 100 m increments along the stream channels. Tag identity (i.e. the mark number code) was recorded when visible, but this was unreliable. Usually only the colour of the tag (corresponding to one of three periods in 2005 and twelve periods in 2006) was identifiable. Sockeye salmon were observed in the tributaries to Skidegate Lake between September 14th and October 15th in 2005, and between September 19th and October 20th in 2006.

The interval between the date of marking and date observed on the spawning grounds was calculated for each marked fish observed. Actual day marked was used when tag identity (i.e. the mark number codes) was visible during spawner observations. For the majority of cases, only the colour codes were visible. In these cases, the tag was assigned a mean marking date (weighted by the numbers of fish marked on each day of period).

Statistical analyses of marked spawner data were performed using JMP 7.0.2 (SAS Institute Inc.). Mean marking dates were compared using Tukey-Kramer tests. Least squares regression analysis was used to test significance of correlation of marine exit period with spawning period and residence time. The assumption of normality for linear regression was tested using the Shapiro-Wilk test. In cases where data failed the Shapiro-Wilk test, data were log transformed prior to statistical testing.

2.3.4 Thermal Regime

Temperatures encountered by fish between marine exit and entering the lake tributaries to spawn were measured and recorded using StowAway TidbiT Temperature Loggers (model TBI32, Onset Computer Corp., Pocasset, MA). A temperature data logger was installed at the base of the fish weir to record the temperature of the upriver migration route. Additional temperature data loggers were installed in the deepest section (maximum depth = 19 m) of Skidegate Lake at approximately N 53^{o}5’41.5” W 131^{o}55’32.4”. Data loggers were suspended at 6, 9, 12 and 15 meters of depth by a line anchored with a 10 lb. weight and suspended in the water column by a small float. Temperature readings were logged every 6 hrs between the summer of 2005 and the fall of 2008. Average daily temperatures are reported.

2.4 Results

2.4.1 Marine Exit Timing

Copper Creek sockeye salmon escapement has averaged 11,084 annually and ranged between 3,664 and 22,061 since 1983. The average exploitation rate was 18% in the local FSC fishery over the same period (Figure 2.3). More than 95% of the population enters the stream between April 30 and June 25, with peak migration during the third week of May (Figure 2.4). The mean date by which 50% of the run migrated past the Copper Creek fence site was May 22 (SD = 4.5 days). The median migration dates in 2005 and 2006 were May 26 and May 22, respectively. Marine exit and upriver migration occurred nocturnally with 80% of sockeye salmon passing the Copper fence between midnight (0:00) and 3:00 am with peak migration at approximately 1:00 am (Figure 2.4).

2.4.2 Spawn Timing and Residence Time

A total of 978 sockeye salmon were sampled from the trap at the Copper Creek fish fence during 2005 and 2006, of which 912 were successfully aged from their scales. As many as seven different age classes were detected in Copper Creek sockeye salmon; however, over 95% of the population consisted of 1.2 and 2.2 aged fish (Table 2.1). Older sockeye salmon tended to be marginally larger than younger sockeye salmon (Table 2.2). Mean (± 95% C.I.) fork length of 1.2 and 2.2 aged sockeye salmon from 2005 was 517.0 ± 31.2 mm and 520.6 ± 27.9 mm ($n = 399$, $p = 0.27$) respectively. In 2006, mean fork length was 501.6 ± 26.4 mm and 512.1 ± 28.2 mm ($n = 483$, $p < 0.0001$) for 1.2 and 2.2 aged fish respectively. Fork lengths were significantly smaller overall in 2006 ($n = 882$, $p < 0.0001$) while males and females tended to be similar in size ($n = 759$, $p = 0.104$).

The sex composition for all fish sampled was 451 females, 336 males and 125 unknowns (Table 2.1). The sex ratio was consistent across age classes and was similar in 2005 and 2006. These data consisted of dissected individuals and fish that were sampled while alive and released, whose assignment of sex may be biased towards females. The rate of unknowns was lower in 2006 due to improved sex identification criteria developed in 2005 when sexes were validated by dissection.

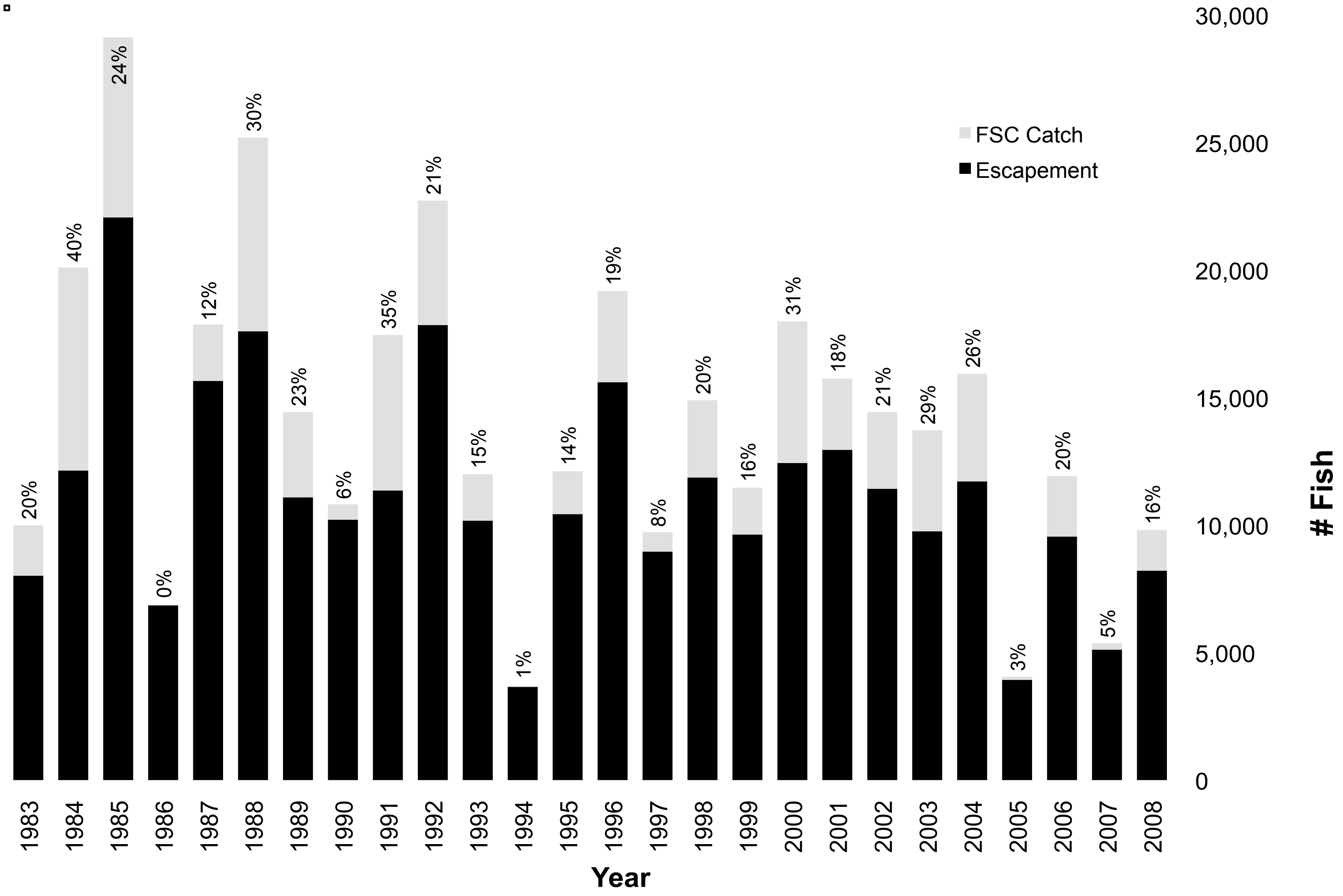

Figure 2.3 Historical run size of sockeye salmon returning to Copper Creek. Black bars represent the total number of fish that escaped to the stream. Light bars represent the catch in the aboriginal food social and ceremonial (FSC) fishery. Percentages above the bars denote the exploitation rate.

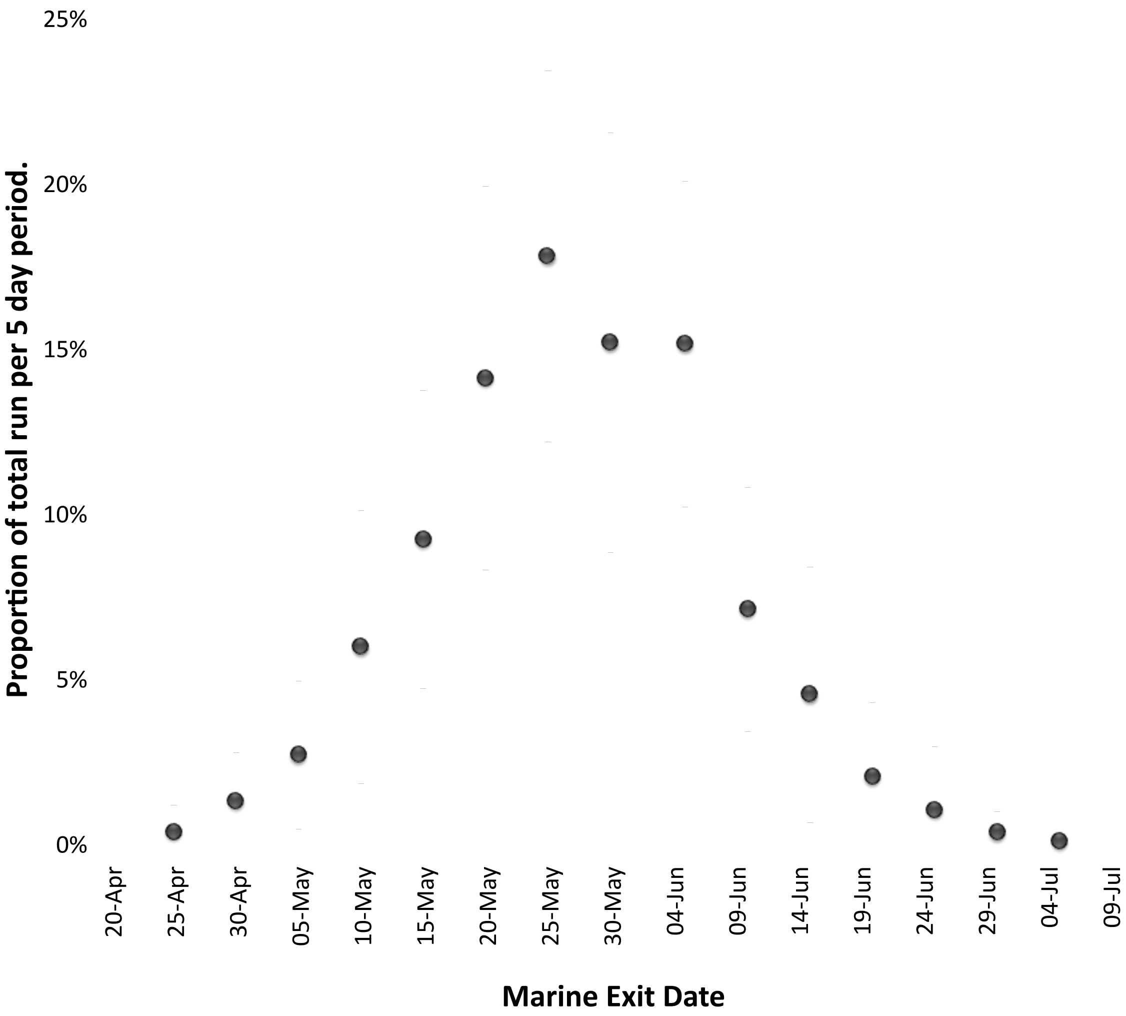

Figure 2.4 Proportion of the total migratory run by five-day period for data between 1983 and 2008. Error bars represent 1 S.D.

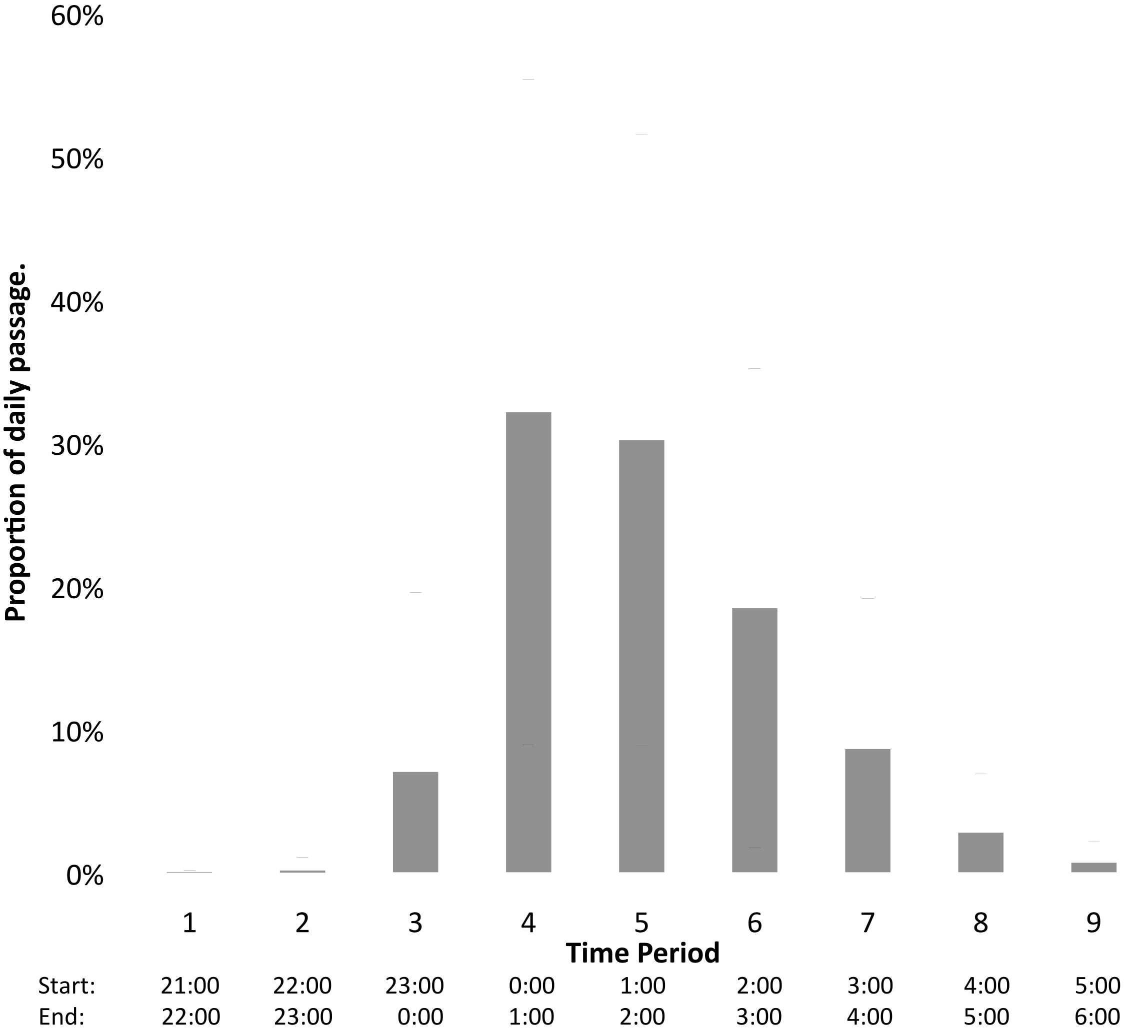

Figure 2.5 Proportion of total daily passage past the enumeration site for data between 2002 – 2006. Error bars represent 1 S.D.

Table 2.1 Sex and age class distribution of adult sockeye salmon returning to Copper Creek in 2005 and 2006.

	Age Class							No.
Sex	1.1	1.2	1.3	2.1	2.2	2.3	3.2	Sampled
2005								
female		63%	6.8%	1.1%	29%			177
male		67%	1.5%	3.0%	28%			134
unk.		54%	1.8%		45%			110
Total		**62%**	**3.8%**	**1.4%**	**33%**			**421**
2006								
female		59%	0.7%		38%	0.7%	0.7%	274
male		65%			34%			202
unk.	6.7%	73%			20%			15
Total	**0.2%**	**62%**	**0.6%**	**0.2%**	**36%**	**0.4%**	**0.4%**	**491**
ALL	**0.1%**	**62%**	**2.1%**	**0.8%**	**35%**	**0.2%**	**0.2%**	**912**

Table 2.2 Mean fork length and weight of sockeye salmon returning to Copper Creek in 2005 and 2006.

	Fork Length (mm)				Weight (g)			
Sex	n	mean	±	95% C.I.	n	mean	±	95% C.I.
2005								
female	185	513.8	±	4.9	68	1626	±	77
male	138	514.4	±	6.3	53	1636	±	83
Unk.	117	528.4	±	4.8	0			
Total	**440**	**517.9**	**±**	**3.2**	**121**	**1630**	**±**	**56**
2006								
female	302	503.9	±	3.0	40	1653	±	75
male	221	509.2	±	3.9	29	1634	±	86
unk.	15	488.3	±	19.8	2	1836	±	698
Total	**538**	**505.6**	±	**2.4**	**71**	**1650**	±	**57**
ALL	**978**	**511.1**	**±**	**2.0**	**192**	**1637**	**±**	**41**

Sockeye salmon spawners were visually surveyed in Shale, Keats and Parsons Creeks, the main spawning tributaries to Skidegate Lake. Distribution of total sockeye salmon observations between Shale, Keats and Parsons Creeks was 34%, 56% and 10% in 2005, and 47%, 52% and 0.1% in 2006 respectively (Figure 2.6). The aggregate peak spawning date for the Shale, Keats, and Parsons Creek aggregate was October 7, 2005 and October 2, 2006. Spawn timing was similar in Shale and Keats Creeks for both years. However, spawn timing in Parsons Creek was variable. The mark rate was estimated to be 8.1% and 4.6% of the total population in 2005 and 2006 respectively. Frequency of observed marked spawners was 1.9% in 2005 and 0.87% in 2006. The reduced frequency of marks observed on the spawning grounds may have been due to an increase in mortality for marked, versus unmarked, fish.

Analysis of marine exit date versus spawning date yielded mixed results (Figure 2.7). Least squares regression analysis detected a weak negative correlation ($r^2 = 0.29$, $n = 17$, $p = 0.027$) between the day of marine exit and the day observed at the spawning grounds in 2005. A multivariate scatterplot matrix ($\alpha = 0.95$) identified a point from the late marine exit group that spawned early, as an influential data point (labelled in Figure 2.7). This was confirmed by a comparison of Cook's distance (0.58), which was greater than the 50th percentile (0.48) of an F distribution ($n = 17$, $df = 1$). When the data were reanalysed without this influential data point, the correlation became insignificant ($r^2 = 0.10$, $n = 16$, $p = 0.24$). In 2006, marine exit date and spawning date were clearly not correlated ($r^2 = 0.02$, $n = 40$, $p = 0.42$) when a stronger data set was used. The number of mark groups increased from three in 2005 to twelve in 2006, and resulted in a 2.7 fold increase in marks observed as spawners.

Residence times from peak marine exit date to peak spawning date were estimated to be 134 and 133 days in 2005 and 2006, respectively. The residence time of marked fish ranged from 83 days to 163 days. Least squares regression analysis detected a significant negative correlation between marine exit date and stream residence time during 2005 ($r^2 = 0.88$, $n = 16$, $p < 0.0001$) and 2006 ($r^2 = 0.71$, $n = 40$, $p < 0.0001$) (Figure 2.8).

2.4.3 Thermal Regime

Typical daily mean stream water temperature of Copper Creek measured at the fish weir ranged between 7^{o}C and 14^{o}C between the first week of May and the end of June between 2006 and 2008. Mean daily water temperature during the sockeye salmon migration period was 12.3^{o}C, 11.2^{o}C and 11.1^{o}C in 2006, 2007 and 2008 respectively. Maximal stream temperatures occurred for short periods (4-6 days) during the months of July and August and typically did not exceed 17.5^{o}C (Figure 2.9).

Skidegate Lake typically became stratified during the month of April, as the lake warmed in spring. Thermal stratification was maintained through the summer until October when the layers “mixed” as the lake cooled in late fall. Water temperatures were highest near the surface (6 m depth) and were typically between 17^{o}C and 20^{o}C during mid summer. Water at deeper depths (15 m), rarely exceeded 10^{o}C (Figure 2.10).

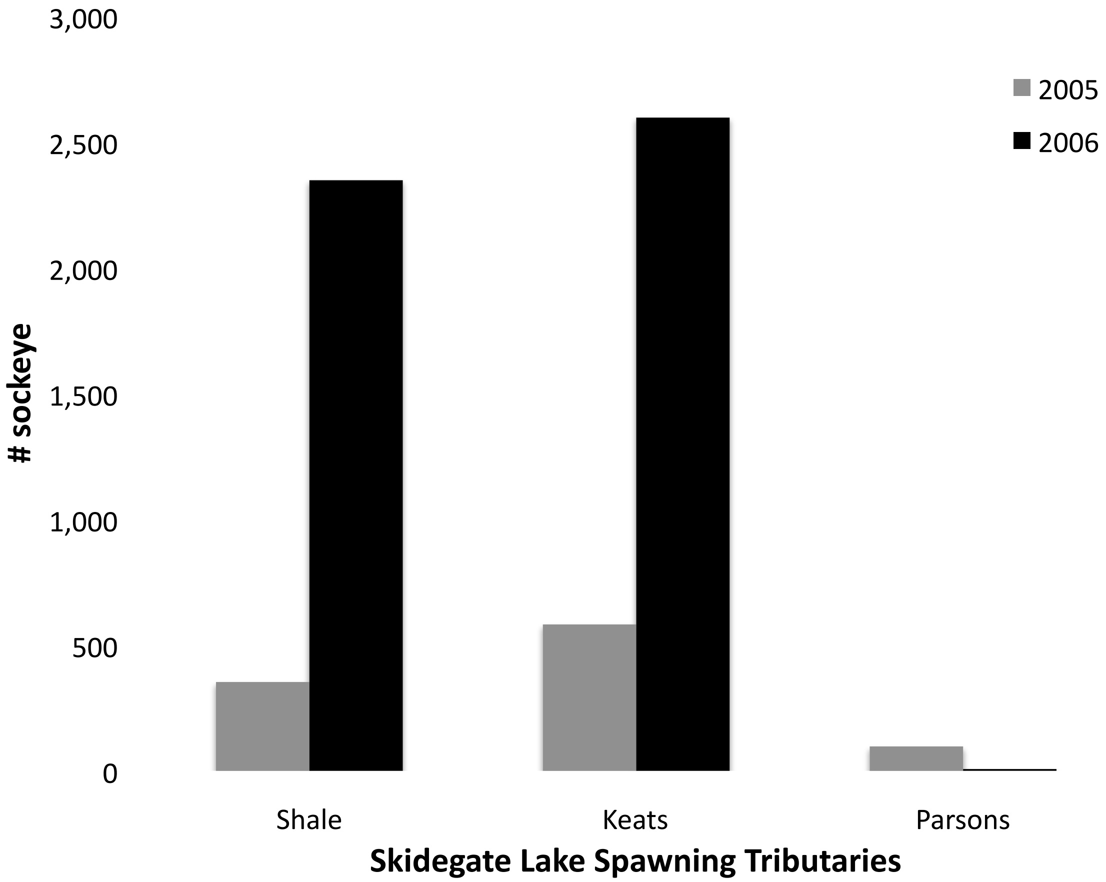

Figure 2.6 Distribution of total sockeye salmon spawner observations within the main spawning tributaries of Skidegate Lake.

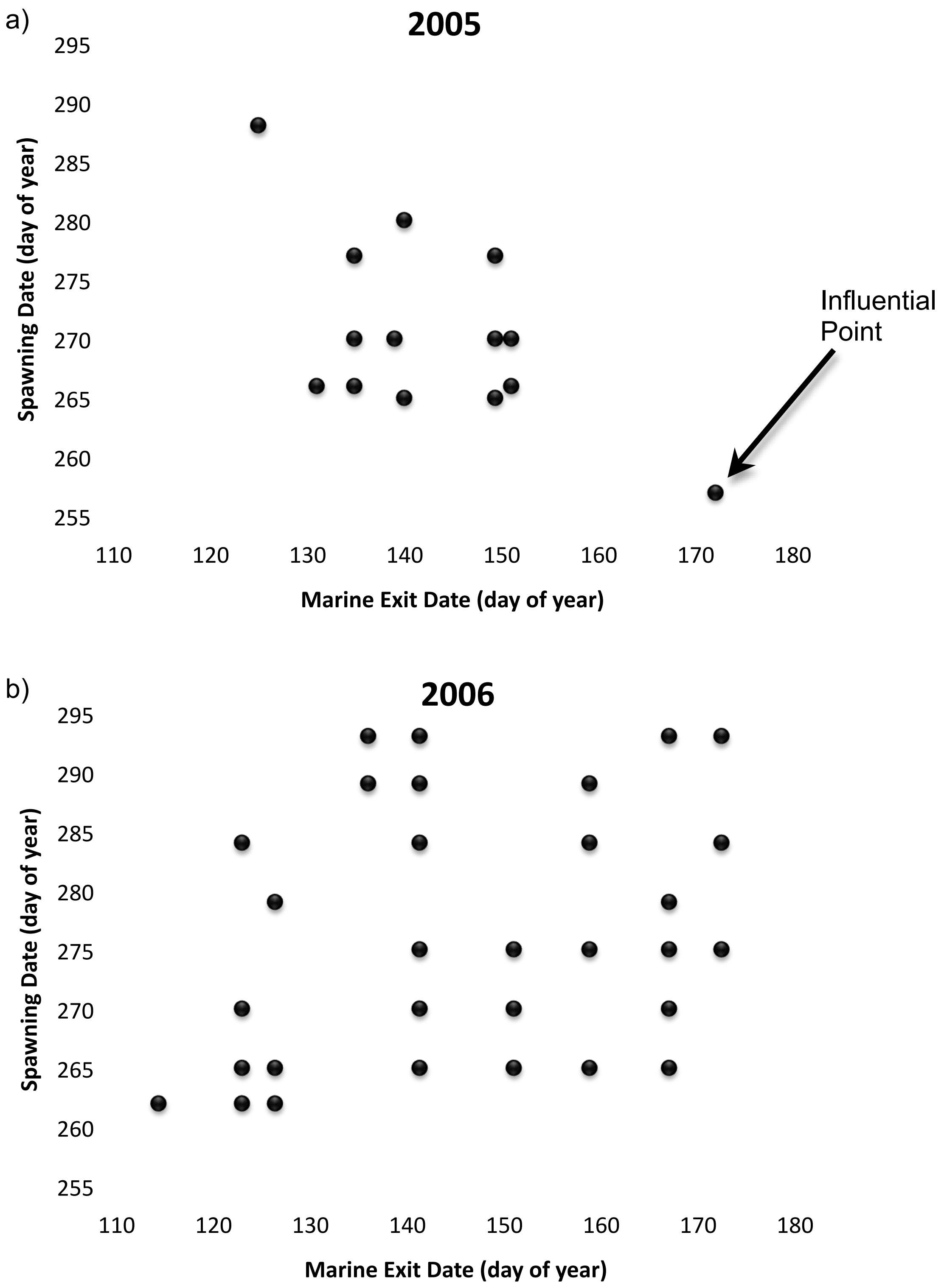

Figure 2.7 Day of the year that marked sockeye salmon were observed on the spawning grounds versus the day they were marked at the fence site at marine exit. (2005: $r^2 = 0.29$, n = 17, p = 0.027; 2006: $r^2 = 0.02$, n = 40, p = 0.42)

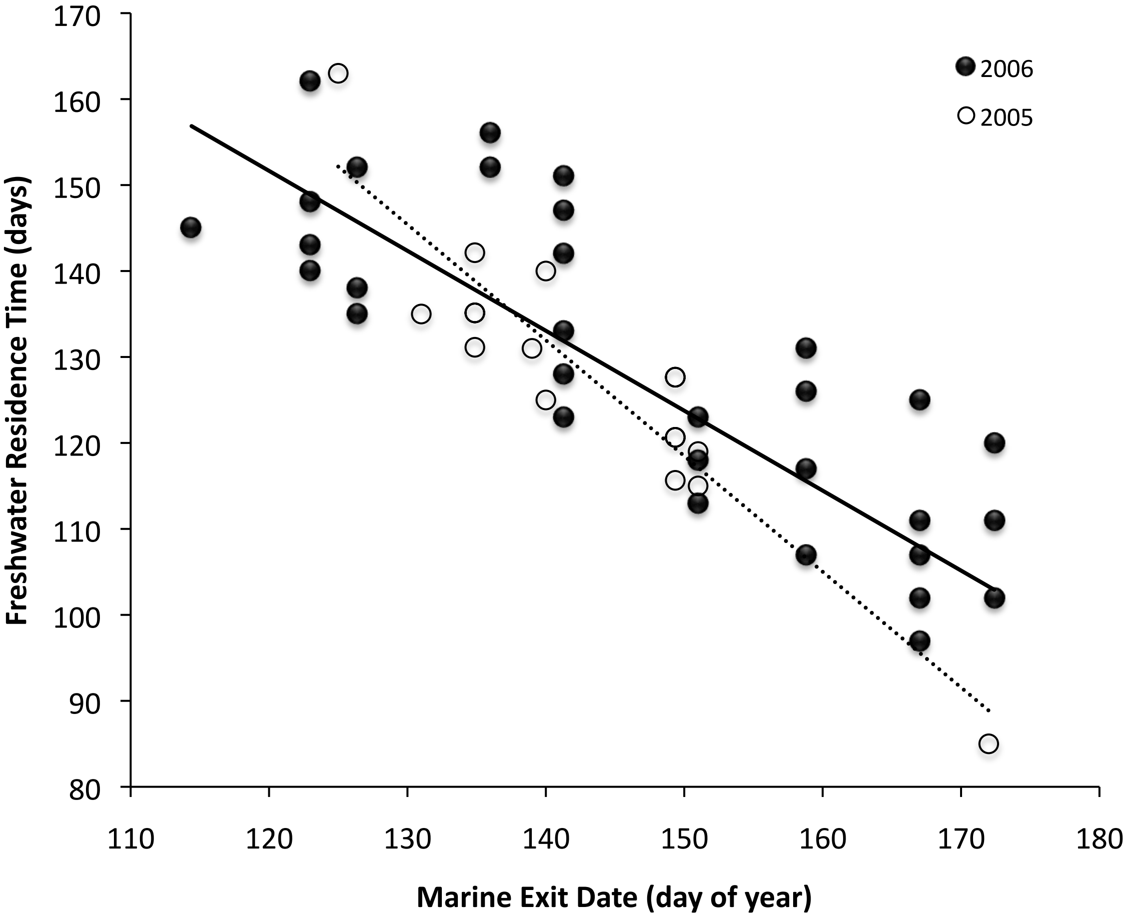

Figure 2.8 Freshwater residence time of marked sockeye salmon at Copper Creek. Residence time refers the number of days between the date fish were marked at marine exit and the day they were observed on the spawning grounds. The dotted and solid black lines represent the regression lines fitted to data from 2005 and 2006 respectively. (2005: $r^2 = 0.88$, $n = 16$, $p < 0.0001$; 2006: $r^2 = 0.71$, $n = 40$, $p < 0.0001$)

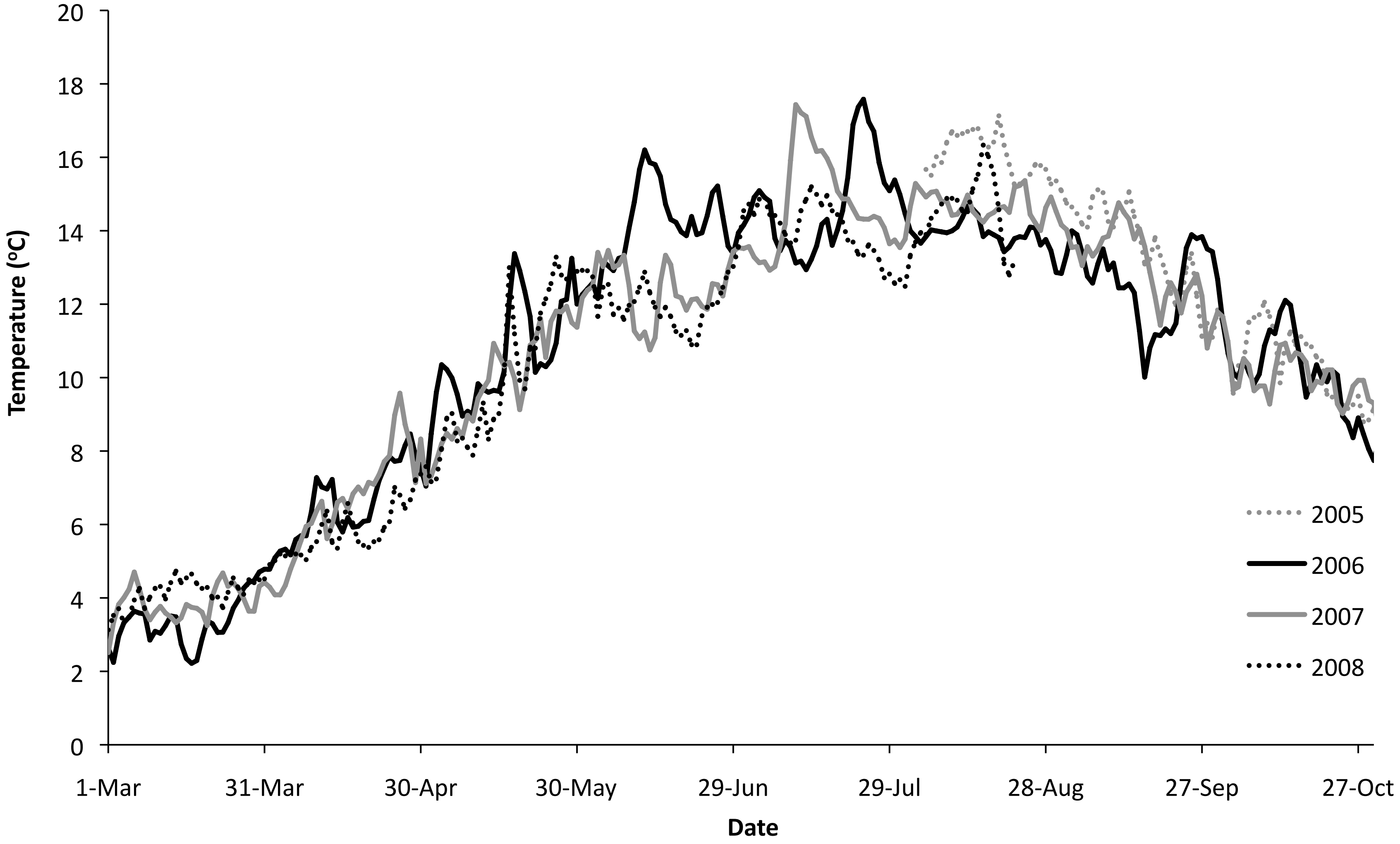

Figure 2.9 Temperature profile of Copper Creek at site of fish weir between 2005 and 2008.

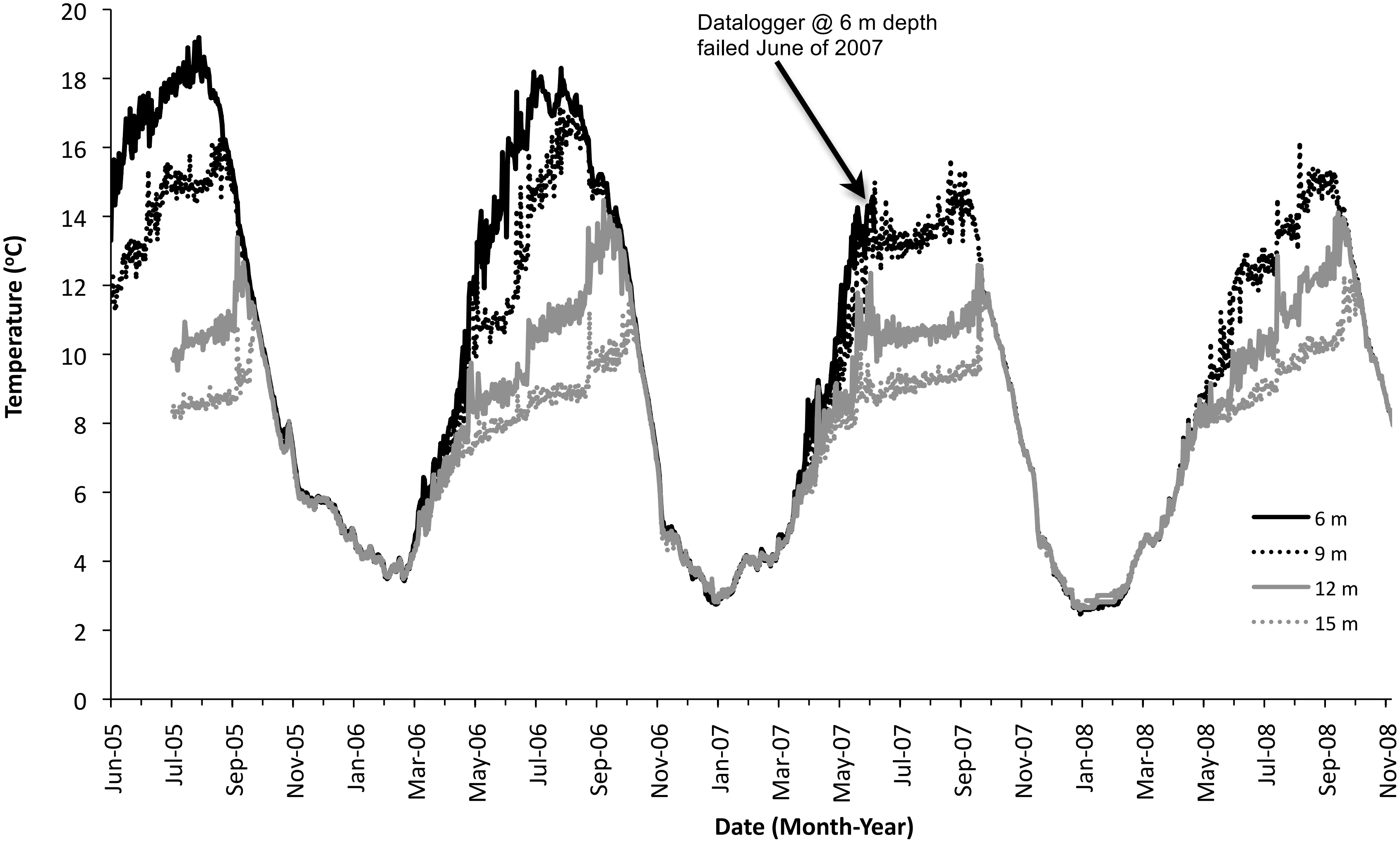

Figure 2.10 Average daily temperature at various depths within Skidegate Lake (max depth = 19m), illustrating the thermal options available to holding sockeye salmon.

2.5 Discussion

This chapter provides a detailed account of the marine exit and spawn timing of a sockeye salmon population that has some of the longest adult freshwater residencies of any population. The data presented here show that ‘early run’ sockeye salmon of Copper Creek (Haida Gwaii) exit the marine environment during May and June, and spend a long period (more than 130 days, on average) in Skidegate Lake before spawning early in October. Marine exit timing has been very consistent at the population level as the inter-annual variation (1 S.D.) associated with the mean median population marine exit date was equal to 4.5 days over the last 25 years. The earliest and latest marine exiting individuals were separated by 75 days, with 95% of all individuals exiting over approximately 56 days.

Copper Creek sockeye salmon are present on their spawning grounds for approximately 30 days between mid-September and mid-October, a much narrower time period than the 55 days of marine exit. The actual spawning period of this population is likely much shorter as males typically arrive on the spawning grounds before females to establish territories (Morbey 2000) and females actively defend their redds after spawning until senescence (Fleming and Gross 1994, Foote 1990, Quinn 2005). The difference in the marine exit versus spawning periods, as well as the lack of correlation between the two periods, results in freshwater residence times that were strongly correlated with marine exit date. Individuals with an early marine exit strategy have much longer residence times (up to 60 days longer) in the lake compared to sockeye salmon with late marine exit strategies.

Furthermore, while the results from 2005 were weak, the stronger data set from 2006 supported the first prediction that date of marine exit was not correlated to spawning date. This is similar to Lake Washington sockeye salmon which have an early migration and long lake residence time prior to spawning (Newell 2005). Despite tremendous variability in individual marine exit timing, individuals were able to spawn at any time (early or late) regardless of their marine exit strategy. It does not appear that reproductive timing games such as protandry (Morbey 2000, Morbey and Ydenberg 2001), competition for mates and high quality nest sites (Fleming and Gross 1994), and nest guarding by females (Gross 1991) on the spawning grounds influences the marine exit strategies among individuals in this population. This data suggests that the adaptive processes that determine timing of marine exit are separate from those influencing the timing of spawning in sockeye salmon populations with early marine exit timing and long delays prior to spawning.

Secondly, Hodgson and Quinn's (2002) migration timing strategies were unable to explain the early marine exit timing and long residence time of sockeye salmon returning to Copper Creek, as fish experience relatively mild temperatures (7 - 14^{o}C) during their short and easy migration to their natal lake. Even during mid-summer, maximal stream temperatures rarely exceed 17.5 ^{o}C, which is moderate and does not pose a risk to migrating sockeye salmon (Farrell et al. 2008). While marine exit and upriver migration to Skidegate Lake occurred nocturnally, daily stream temperature only ranged by 1.0^{o}C (1 S.D. = 0.6 ^{o}C) between night-time minimums and mid-day maximums in the months between May and August from 2006 to 2008. Once in their natal lake, fish had a range of thermal choices including cooler water temperatures (thermal refuge) at the bottom of the lake (Figure 2.10). Copper Creek sockeye salmon likely thermoregulate behaviourally to maximize their metabolic efficiency, similar to early-run Lake Washington sockeye salmon (Newell and Quinn 2005).

Inter-annual variation of migration timing within salmon populations has been commonly explained by a temperature-displacement model introduced by Blackbourn (1987). He further hypothesized that salmon have a sense of date (Gilhousen 1960) and can orient themselves (Quinn 1982) and therefore begin their homeward migration at a population specific date which is genetically determined (Quinn et al. 2000, Smoker et al. 1998). This was further supported by Hodgson et al. (2006), who concluded that the date when salmon initiate homeward migration is a population-specific trait, largely unaffected by the fish's location at sea, suggesting that the variation in marine exit date of a salmon population is a function of its distribution at sea and the resulting differences in migration distance.

Recent studies of Fraser River sockeye salmon have linked sockeye salmon body condition to different marine exit strategies and their resulting river migration survival probabilities (Cooke et al. 2006a, Cooke et al. 2006b, Cooke et al. 2004, Crossin et al. 2009, Crossin et al. 2007, Crossin et al. 2008, Young et al. 2006). The data from this study suggests that an early marine exit strategy may be energetically costly considering the variation in freshwater residence time among early and late exit strategies. These costs arise from the forgone feeding opportunities of marine food resources that increase through the spring and peak during early summer (Brodeur et al. 1996), as well as the metabolic cost of increased freshwater holding times prior to spawning. While the date when salmon initiate homeward migration is a population-specific adaptation, it may also condition dependent. In this scenario, an individual sockeye salmon could accelerate or delay the initiation of homeward migration based on the reproductive benefits associated with continued feeding at sea trading off the increased mortality risk from exposure to predation. While the seasonal variability of marine predation is unknown, this hypothesis assumes that the relative cost of marine predation is seasonally constant relative to the cost of upriver migration.

Copper Creek sockeye salmon would be a useful model system for examining the condition-dependent variation of migration timing within a population because the confounding effects of spawning, such as reproductive timing games, appear to be strategically independent. Marine growing conditions prior to homeward marine migration likely influences the body condition of returning sockeye salmon. Body size, growth rate and energy reserves may act as measures of body condition allowing comparisons to marine exit strategies. This may provide insight into the role of condition dependence at the initiation of homeward migration.

2.6 Conclusion

The thermally based migration strategies, proposed by Hodgson and Quinn (2002) to explain early migration timing and long wait times prior to spawning for coastal sockeye salmon populations do not appear to apply to sockeye salmon returning to Copper Creek. Theories that use thermal limitations during freshwater migration are based on a trade-off between temperature-driven metabolic costs and finite energy reserves for migration and reproduction. It appears there is an alternative cost to upriver migration that may be driving the trade-off associated with the early marine exit timing and long wait times of sockeye salmon returning to Copper Creek and potentially other Haida Gwaii populations.

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CHAPTER 3: CONDITION-DEPENDENCE IN THE MARINE EXIT TIMING OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) RETURNING TO COPPER CREEK, HAIDA GWAII

3.1 Abstract

The individual variation of marine exit timing (river entry) of an early-run sockeye salmon population that has long delays between upriver migration and spawning was examined using a basic life history model. Populations with long delays before spawning are likely good candidates for studying the condition-dependence of marine exit because they lack the confounding effects of reproductive timing games associated with spawning. Body condition parameters such as growth rate, lipid density, age class (2.2 vs. 1.2), sex, gonad size and fecundity (# eggs) were correlated with the date of marine exit. Individuals with early marine exit had higher growth rates in the months prior to river entry, greater lipid density, were more likely to be male, were more likely to be of the 2.2 vs. 1.2 age class, had smaller gonads, but (if female) had larger number of (smaller) eggs. These trends were explained using a simple life history model and support the hypothesis that marine exit timing is a condition-dependent life history decision.

3.2 Introduction

The timing of homeward migration has been shown to be a heritable trait in salmonid fishes (Hansen and Jonsson 1991, Quinn et al. 2000, Smoker et al. 1998). Natural selection can therefore act on this trait to maximize the probability of successful migration and subsequent spawning (Quinn and Adams 1996). Presumably, this timing depends on the long-term average of environmental conditions and seasonal variation that influence the probability of successful reproduction.

The initiation of homeward migration from the open ocean is considered to be a population-specific “genetic switch”, regulated by photoperiod (Gilhousen 1960, Quinn 1982), and is largely unaffected by location at sea (Gilhousen 1960, Hodgson et al. 2006). In essence, this model suggests that intra-population variation in marine exit date is a product of the oceanic distribution of individuals at the moment that homeward migration is initiated. As a result, individuals closer to their natal stream arrive earlier than those further away. This displacement model has also been used to explain inter-annual variation in median population marine exit date (river entry) of Fraser and Bristol Bay sockeye salmon. These differences were attributed to changes in latitudinal distribution in the North Pacific during “warm” versus “cold” winters prior to homeward migration (Gilhousen 1960, Hodgson et al. 2006).

Recent work however, has demonstrated that body condition parameters, such as energetic and reproductive state, are important determinants of marine exit timing and reproductive success of some Fraser sockeye salmon populations (Cooke et al. 2008a, Cooke et al. 2006a, Cooke et al. 2006b, Cooke et al. 2008b, Crossin et al. 2009, Crossin et al. 2007, Crossin et al. 2008, Young et al. 2006). This suggests that individual marine exit timing may also be condition dependent and is therefore a behavioural strategy based on an evolved life history trade-off.

Individual marine exit date within a population can be viewed in fitness-maximizing terms, namely as an evolved life history decision influenced by: (a) marine growth opportunities, (b) mortality costs in the ocean prior to marine exit, and (c) by the cost of upriver migration. Analogous to age at maturity models, marine exit is predicted to occur when the marginal fitness benefits and costs of prolonging ocean residence are equal. For instance, maturation is considered a conditional strategy in age at maturity models and may be delayed when growth is poor (Bilton et al. 1982, LaLanne 1971, Lewis 1987, Parker and Larkin 1959, Peterman 1985). This is due to the fitness benefits derived from growth and accumulation of energy reserves during prolonged ocean residence. Specifically, the improved reproductive success attributed to larger body size and energy reserves, such as successful migration to spawning grounds, competition, spawning behaviour, and fecundity (Fleming and Gross 1994, Gross 1985, van den Berghe and Gross 1984). These reproductive benefits must be weighed against the potential increased mortality experienced with extended sea residence as well as the changes in up-river migration costs associated with different marine exit timing (e.g. temperature, flow, disease, predation, etc.).

In this study, the condition dependence of marine exit timing strategies (i.e. entrance to freshwater and start of upstream river migration) is investigated in a population of early run sockeye salmon returning to Copper Creek, British Columbia. The tagging data presented in Chapter 2 show that this population has some of the longest known delays (mean 134 d) between marine exit and spawning (Hodgson and Quinn 2002). This effectively decouples marine exit from spawning, so that all spawning options are available to individuals regardless of their marine exit strategy. Early-run sockeye salmon populations that experience long delays between upriver migration and spawning are therefore good candidates to study the condition dependence of marine exit without the complicating effects of spawn timing games and behaviours (Morbey 2000, Morbey and Ydenberg 2003, Morbey and Ydenberg 2001).

While body condition or state can be influenced by a wide range of environmental and genetic attributes, body size, growth rate, energy density and age class are integral parts of growth and body condition processes that influence this life history trade-off. Individuals that have experienced “good” marine growing conditions are able to allocate more resources to growth and subsequently to their body size or to energy reserves thereby reducing the marginal fitness benefits of delayed marine exit. Similarly, older individuals typically have a size advantage to younger cohorts, and therefore have a reduced marginal fitness benefit to delaying marine exit and prolonging marine growth. The marine exit strategy of individuals within a sockeye salmon population is hypothesized to be a life history strategy and is influenced by body condition. More specifically, I predicted that older, larger, fast-growing individuals with high energy reserves will choose an earlier marine exit date because the marginal benefits derived from remaining at sea are less than those gained by younger, smaller, slow growing individuals with low energy reserves.

3.3 Methods

3.3.1 Study Area

Copper Creek sockeye salmon are described in Chapter 2. This population exhibits early marine exit timing and waiting periods in excess of 100 days prior to spawning. These attributes ensure that all individuals of the spawning population have completed their migration and are holding in their natal lake well before they are subjected to reproductive timing games associated with spawning.

3.3.2 Sample Collection

Sockeye salmon were trapped as they returned to Copper Creek at the fence described in Chapter 2 (Figure 2.1). Fish were collected from May 2 to June 26, 2005, and April 24 to June 29, 2006. Totals of 440 and 539 sockeye salmon were sampled in 2005 and 2006, respectively.

Meristics (sex, fork length ± 0.5 cm) and scales (one from each side of the body) for age and growth analysis were collected from 317 fish in 2005 and 442 fish in 2006. Fish were removed from the trap using a cradle net and placed into a foam-covered trough containing water pumped directly from the stream, processed, and released upstream of the fish fence. An additional 123 (2005) and 97 (2006) fish were trapped and euthanized. They were then sexed, measured for fork length and post-orbital hypural length (± 0.1 cm), body mass (± 0.1 g), and five scales collected for age and growth analysis. Gonads were removed and the head cut off approximately 2.5 cm behind the distal edge of the operculum. Mass of gonads and heads were measured using a using a digital field scale (± 0.1 g). Tissue samples were stored in airtight bags, transported to the laboratory and stored at -20°C until analysed.

3.3.3 Lab Analysis

Age and Growth

Acetate impressions of the scales were made using a hydraulic press and visually interpreted by Birkenhead Scale Analysis (Lone Butte, B.C.) to determine age. Fish age is reported using the scheme suggested by Koo (1962), which identifies years spent in freshwater and the ocean. For example, an age reported as 1.2 refers to fish that has spent 1 year in freshwater (fry to smolt) and 2 years at sea (smolt to adult). Circuli counts and distances between annuli were measured on a 20° alignment of the ventro-anterior axis using a projection microscope at 100 X magnification and a Calcomp digitizer. This method is used by the Pacific Salmon Commission and is based on Clutter and Whitesel (1956), and Gamble and Cox-Rogers (1993).

Number of circuli and distances between annuli were used to estimate growth rates. Fork lengths at the 1st and 2nd annulus and the scale edge for each fish was estimated using Fraser-Lee’s formula as suggested by Ricker

(1992). Scales exhibiting resorption up to last marine annulus, where the spring growth following last annulus was not visible, were removed from the analysis. Increases between circuli spacing are associated with increased food availability (Barber and Walker 1988) and are commonly observed to start the next year of growth after the winter annulus during March (pers. comm. Carol Lidstone, Birkenhead Scale Analysis). This is consistent with the annual variability primary production observed in the North Pacific (Brodeur et al. 1996). March 31 was arbitrarily defined as the date at which the year's growth begins. Growth rates were calculated in millimetres per day, as the difference in back-calculated fork length between the beginning and end of a period, divided by the duration of the period. Growth rates are estimated for the first and second years at sea, and the spring before capture. The growth rate during the spring before capture is equal to the difference between the fork length at capture and the back-calculated fork length at the end of the 2nd annulus, divided by the number of days between the date of capture and March 31 of that year.

Gonad Size and Fecundity

Frozen gonads were thawed and reweighed (± 0.1 g) to account for dehydration associated with freezing. Total dry gonad mass was estimated by drying a subsample of tissue at 95°C for 24 hrs. Individual egg size was determined as the mean wet and dry weight of 10 eggs. Fecundity was estimated by dividing the mass of the whole ovary by the mass of a subsample with a known number (~100) of eggs.

The seasonal bias in the method used to estimate the number of eggs is unknown. As individual egg size increased through the season, they became easier to separate from the ovary and count. As such, any bias in this method would underestimate egg number early in the season when eggs were smallest. Therefore, any negative correlations of fecundity with marine exit date are likely conservative.

Energy Density

Frozen samples were thawed and weighed (± 0.1 g) to account for dehydration associated with freezing. A two cm cross section of the body was cut posterior to the head and gill cover. Each cross section was weighed (± 0.1 g), homogenized (Cuisinart Mini-Prep Plus Processor), and a 25 g subsample collected for tissue analysis. In 2006, the remainder of the tissue was combined with the original carcass, viscera and gonads of 18 fish, homogenized in an industrial food processor (Robot Coupe Blixer BX6V), and 25 g subsample of the homogenate withdrawn (used to validate tissue analysis of dorsal cross sections). Lipid, water and carbon contents (%) were determined according to methods outlined by Higgs et al. (1979). Lipid content was determined through a 1:1 chloroform-methanol extraction of homogenized tissue. Water content was determined by difference in weight of a sample of homogenized tissue dried at 95^{o}C for 24 hrs. Carbon was determined by the mass of ash remaining from a sample of dried homogenized tissue after combustion at 600^{o}C for 2 hrs. Protein was calculated as the difference between 100 and the summed percentages of lipid, water and carbon, as in previous studies (Berg et al. 1998, Crossin et al.

2004, Hendry and Berg 1999, Hendry et al. 1999). Lipid concentration (g Kg^{-1} wet weight) was multiplied by 0.03954 MJ Kg^{-1} and protein concentration (g Kg^{-1} wet weight) by 0.02364 MJ Kg^{-1} to calculate their energetic equivalents and summed for total energy density (Higgs et al. 1979).

3.3.4 Data Analysis

Statistical analyses used JMP 7.0.2 (SAS Institute Inc.). Comparisons of means were tested using one-way ANOVA with Tukey-Kramer tests or a two or three factor general linear model (GLM) when testing with age and / or sex as covariables. Homogeneity of variance was tested using O'Brien's test. In cases where violations of homogeneity of variance were detected, the Welch ANOVA for the means was used. Least squares regression analysis was used to test significance of correlations of body size, growth rate, energy density, fecundity (egg number), and gonad size versus marine exit date with age and / or sex as covariables. A general linear model with interaction terms was used to verify that tissue subsamples (dorsal cross section) represent the whole carcass for energy density analysis of somatic tissue. The assumption of normality for linear regression was tested using the Shapiro-Wilk test. In cases where data failed the Shapiro-Wilk test, data were log transformed prior to statistical testing.

3.4 Results

The numbers of sockeye salmon that migrated, past the counting fence at Copper Creek, to spawn were 4,056 and 11,920 in 2005 and 2006, respectively. Returning fish were generally larger and returned later in 2005 than in 2006 (Chapter 2). Differences in fork length were detected between sexes ($n = 488$, $p = 0.0185$) and 1.2 and 2.2 age classes ($n = n = 482$, $p < 0.0001$) in 2006, but not 2005 (Table 3.1). Sockeye salmon of the 2.2 age class were marginally heavier ($n = 109$, $p = 0.031$) than 1.2 aged fish in 2005 but not 2006. Body size, measured as either fork length (2005: $n = 399$, $p = 0.368$; 2006: $n = 491$, $p = 0.914$) or body mass (2005: $n = 109$, $p = 0.125$; 2006: $n = 65$, $p = 0.056$) was not correlated with marine exit date (Figure 3.1 & 3.2).

The overall sex ratio (proportion of females) of Copper Creek sockeye salmon was similar during years sampled. The proportion of females was 56% ($n = 291$) in 2005 and 57% ($n = 468$) in 2006 (Table 3.2). Marine exit date of females was up to a week later than males ($n = 111$, $p = 0.13$ in 2005; $n = 468$, $p < 0.0001$ in 2006). Mean exit date for females was May 27 (S.D. = 15.6 days) and June 1 (S.D. = 16.5 days) in 2005 and 2006 respectively. Mean exit date for males was May 22 (S.D. = 14.3 days) and May 24 (S.D. = 16.5 days) in 2005 and 2006 respectively. The change in sex ratio over the marine exit period is depicted below in Figure 3.3.

Table 3.1 Body size comparisons of sockeye salmon returning in 2005 and 2006. Means connected by the same letter are not significantly different.

			n	Mean	±	95% C.I.	Significance		
2005									
Fork Length (mm)									
	Sex	F	163	512	±	5	A		p = 0.111
		M	128	518	±	5	A		
	Age	1.2	202	515	±	5	A		p = 0.950
		2.2	89	515	±	6	A		
Body Weight (g)									
	Sex	F	60	1582.9	±	76.7	A		p = 0.099
		M	49	1670.8	±	79.6	A		
	Age	1.2	66	1575.8	±	74.9	A		p = 0.031
		2.2	43	1693.9	±	77.9		B	
2006									
Fork Length (mm)									
	Sex	F	288	503	±	3	A		p = 0.0185
		M	200	509	±	5		B	
	Age	1.2	305	502	±	3	A		p < 0.0001
		2.2	177	512	±	4		B	
Body Weight (g)									
	Sex	F	35	1648.5	±	81.1	A		p = 0.650
		M	27	1626.1	±	96.8	A		
	Age	1.2	42	1645.9	±	71.5	A		p = 0.559
		2.2	22	1643.0	±	123.4	A		

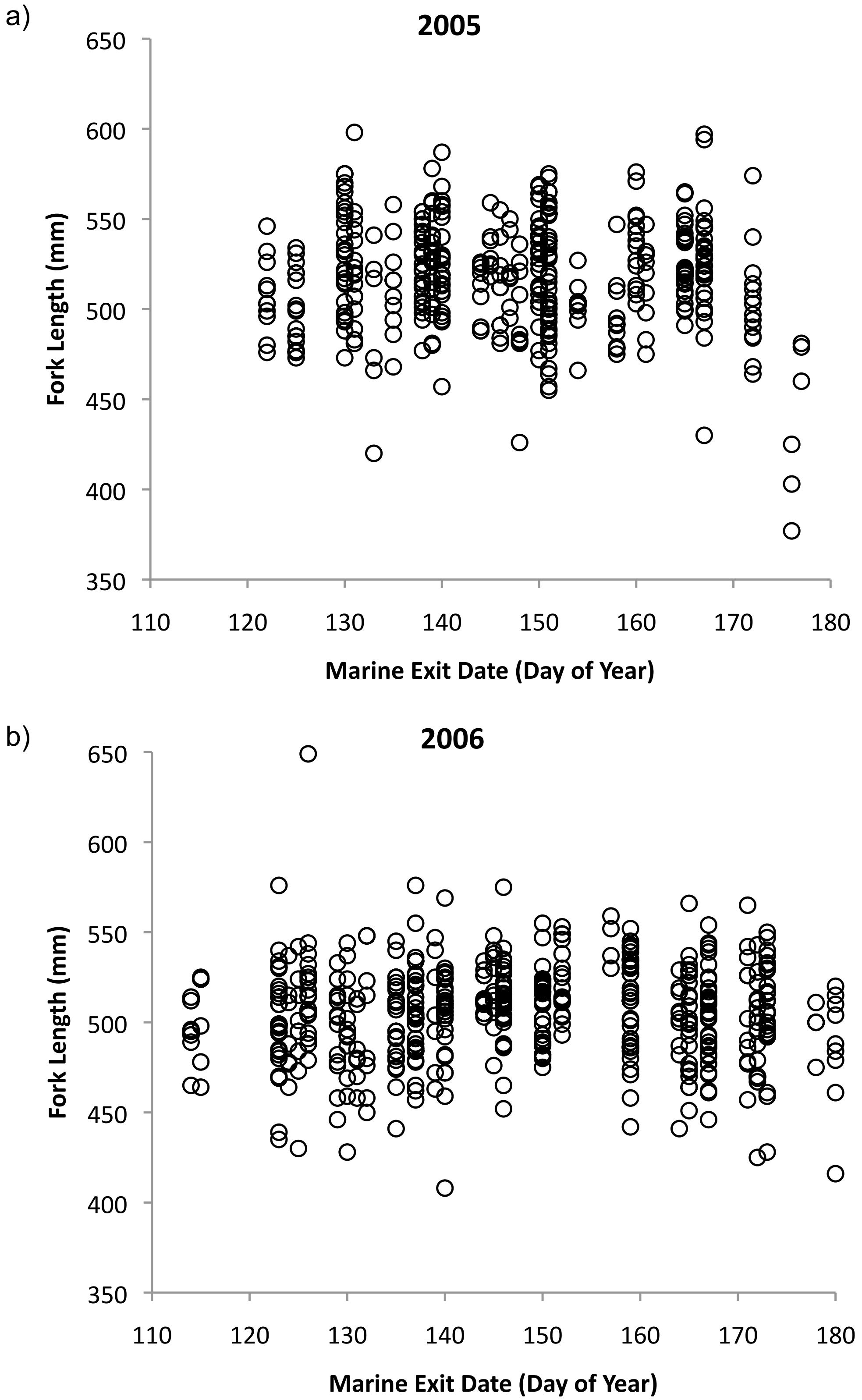
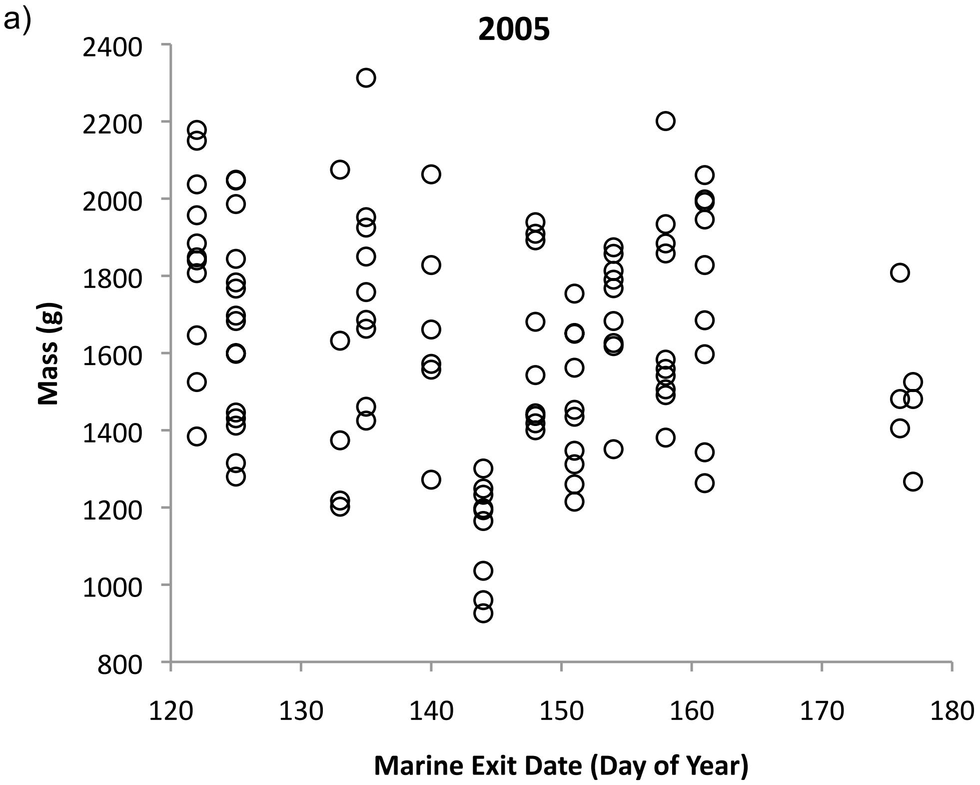


Figure 3.1 Fork length by exit day for sockeye salmon returning in a) 2005 (n = 399, p = 0.368) and b) 2006 (n = 491, p = 0.914).

a)



b)

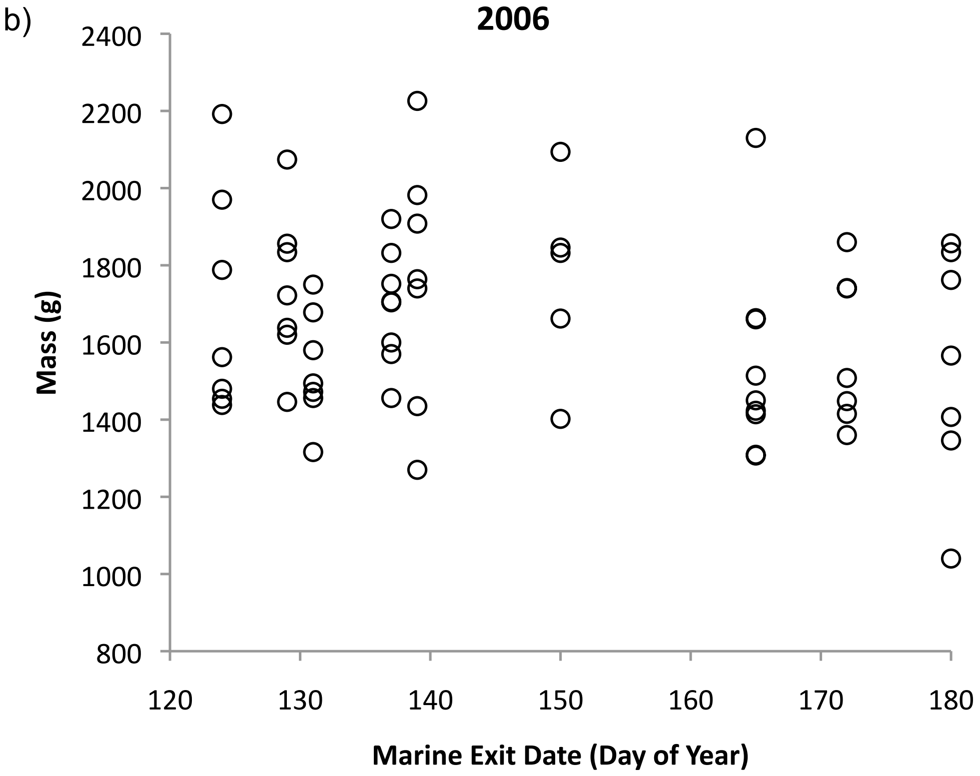
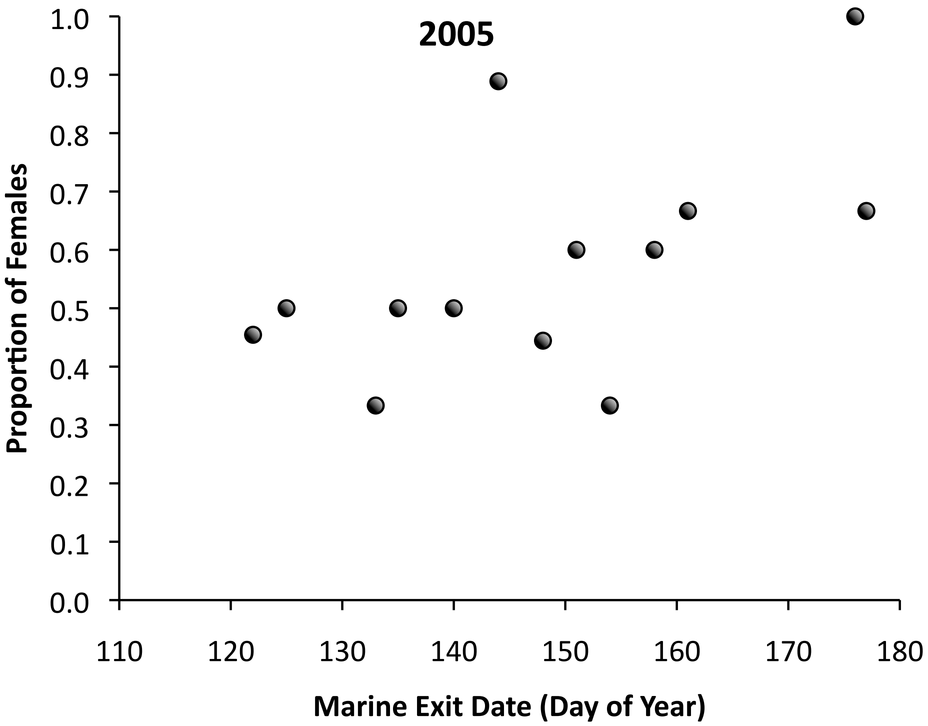


Figure 3.2 Body mass by exit day for sockeye salmon returning in a) 2005 (n = 109, p = 0.125) and b) 2006 (n = 65, p = 0.056).

Table 3.2 Sex and age class ratios by year for sockeye salmon in 2005 and 2006.

			Proportion by Sex		Proportion by Age	
Year	Age	Sex	n	%	n	%
2005						
	1.2	F	112	55%	259	65%
		M	90	45%		
	2.2	F	51	57%	140	35%
		M	38	43%		
2006						
	1.2	F	163	55%	304	63%
		M	131	45%		
	2.2	F	105	60%	179	37%
		M	69	40%		

a)



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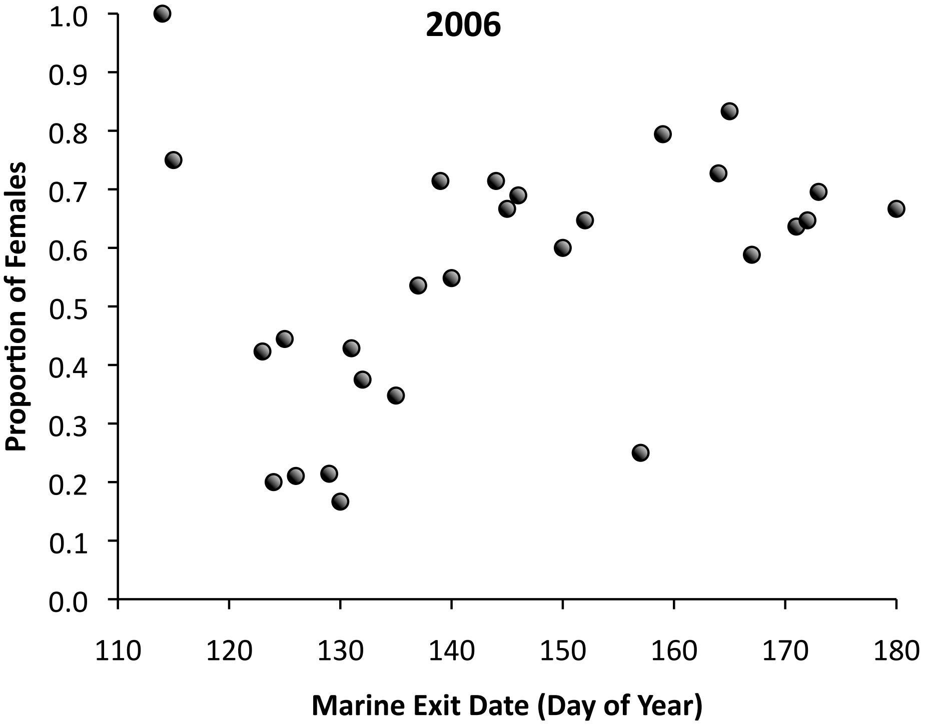


Figure 3.3 Proportion of females by marine exit date in a) 2005 and b) 2006. Each point represents the proportion of females in a day's catch. Sample sizes ranged from 3 to 34. Mean exit date for males was 4.3 and 7.4 days earlier than females in 2005 and 2006 respectively ($n = 111$, $p = 0.13$ in 2005; $n = 468$, $p < 0.0001$ in 2006).

The 1.2 to 2.2 age class ratio was similar during years sampled with the proportion of 1.2 vs. 2.2 aged sockeye salmon equal to 65% (n = 399) in 2005 and 63% (n = 483) in 2006 (Table 3.2). Mean exit date of younger 1.2 aged fish was 10 days later in 2005 and 6 days later in 2006 compared to older 2.2 aged fish (n = 399, $p < 0.0001$ in 2005; n = 483, $p = 0.0004$ in 2006). Mean exit date of the 1.2 age class was June 1 (S.D. = 13.3 days) and May 31 (S.D. = 16.6 days) in 2005 and 2006 respectively. Mean exit date of the 2.2 age class was May 22 (S.D. = 12.8 days) and May 25 (S.D. = 17.9 days) in 2005 and 2006 respectively. The change in age class ratio over the marine exit period is depicted in Figure 3.4 below.

For comparisons of growth rate, scale samples that had signs of resorption (codes > 2) were removed from the analysis. A total of 192 (44%) and 214 (48%) of available samples were rejected in 2005 and 2006 respectively. The probability of rejection due to resorption was not correlated (logistic regression; 2005: n = 399, $p = 0.44$; 2006: n = 483, $p = 0.18$) with marine exit date. It is therefore unlikely that methods used to reject samples due to resorption have biased the back calculations of fork length and growth rates with respect to marine exit.

Back-calculated fork lengths were found to be significantly different between age groups, but not sexes in Copper Creek sockeye salmon caught during 2005 and 2006 (Figure 3.5). In general, 1.2 aged sockeye salmon smolts entered the sea at a smaller size (10 – 20 % smaller) compared to their 2.2 aged cohorts. These back-calculated fork lengths were consistent with actual fork length measurements of sockeye salmon smolts collected between 1997 and 2000 (Haida Fisheries Program unpublished data). While the relative difference in fork length between age groups diminished as they grew at sea, 1.2 aged fish were generally smaller compared to their 2.2 aged cohorts at marine exit.

Analysis of log transformed growth rate data found that growth rates during the first or second year at sea were not correlated with marine exit date for sockeye salmon returning in 2005 (n = 204, p = 0.22 -1st year at sea; n = 204, p = 0.18 - 2nd year at sea) or in 2006 (n = 263, p = 0.23 - 1st year at sea; n = 263, p = 0.79 - 2nd year at sea). However, growth rate during the spring prior to capture was negatively correlated with marine exit date when tested with a 2-factor regression model using age class as a covariate (2005: r^2 = 0.17, n = 204, date p < 0.0001, age p = 0.029; 2006: r^2 = 0.11, n = 263, date p < 0.0001, age p = 0.009; Figure 3.6). With the exception of males of the 1.2 age class in 2006, growth rates were not found to be significantly different between individual age class – sex groups when means were compared with one-way ANOVA (Table 3.3). Males had greater mean growth rates (n = 263, p = 0.0068) compared to females in 2006 when growth rate was compared with age and sex (2-factor GLM).

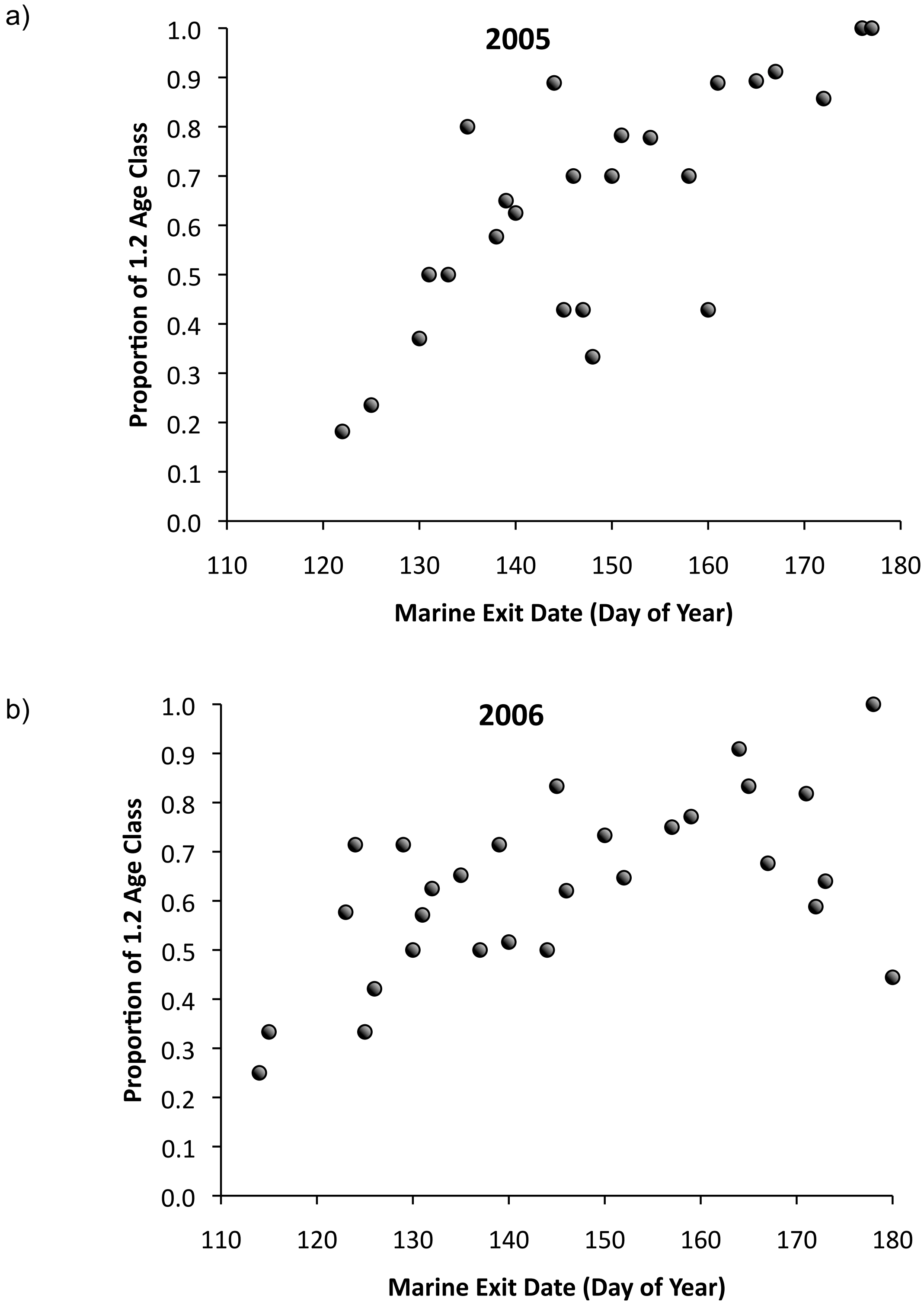
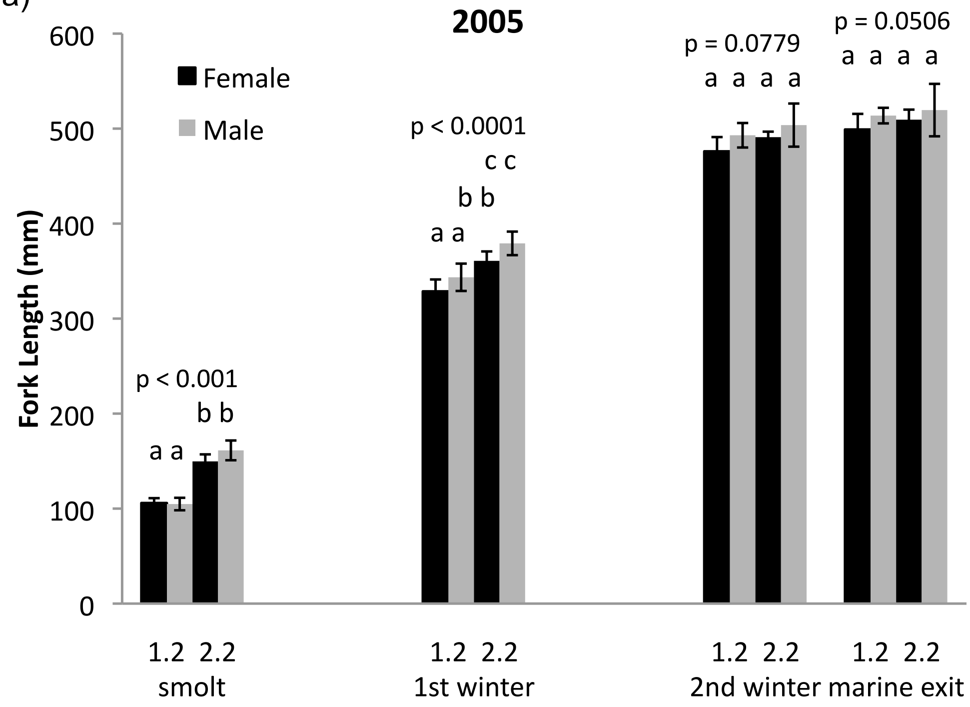


Figure 3.4 Proportion of 1.2 versus 2.2 aged sockeye salmon by exit date returning in a) 2005 and b) 2006. Each point represents the proportion of 1.2 aged fish in a day's catch. Sample sizes ranged from 3 to 46. Mean exit date of younger 1.2 aged fish was 10 days later in 2005 and 6 days later in 2006 compared to older 2.2 aged fish (n = 399, $p < 0.0001$ in 2005; n = 483, $p = 0.0004$ in 2006).

a)



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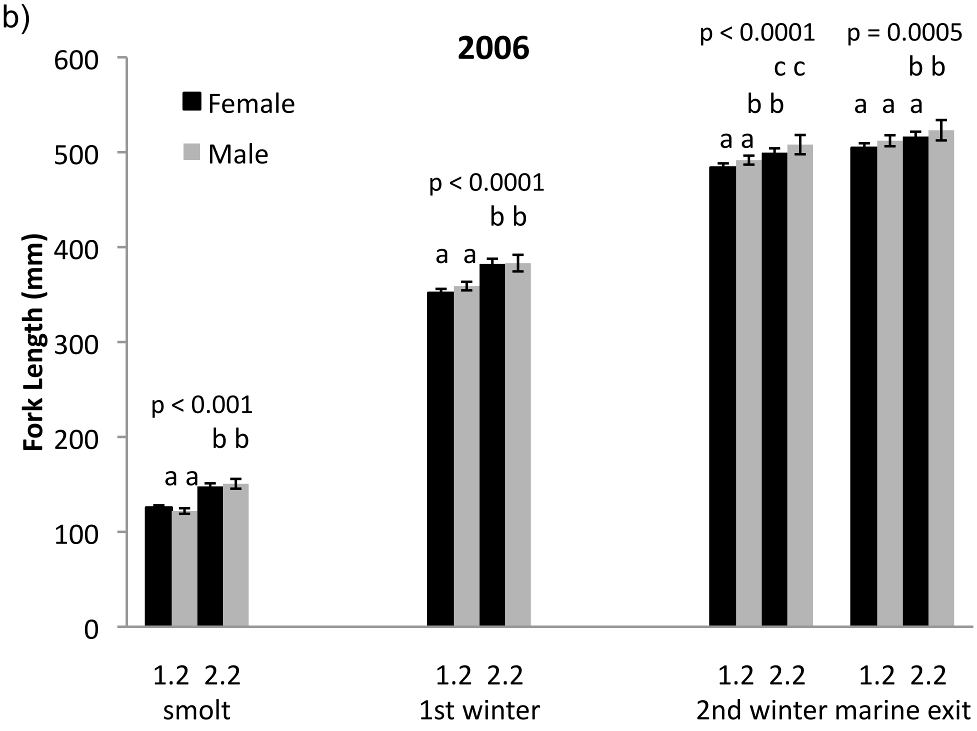


Figure 3.5 Fork lengths at smolting, 1st and 2nd winter at sea, and marine exit for individuals captured in a) 2005 (n = 580) and b) 2006 (n = 263). Fork lengths back calculated from scales samples. Means compared using 1-way ANOVA. Means connected by the same letter are not significantly different.

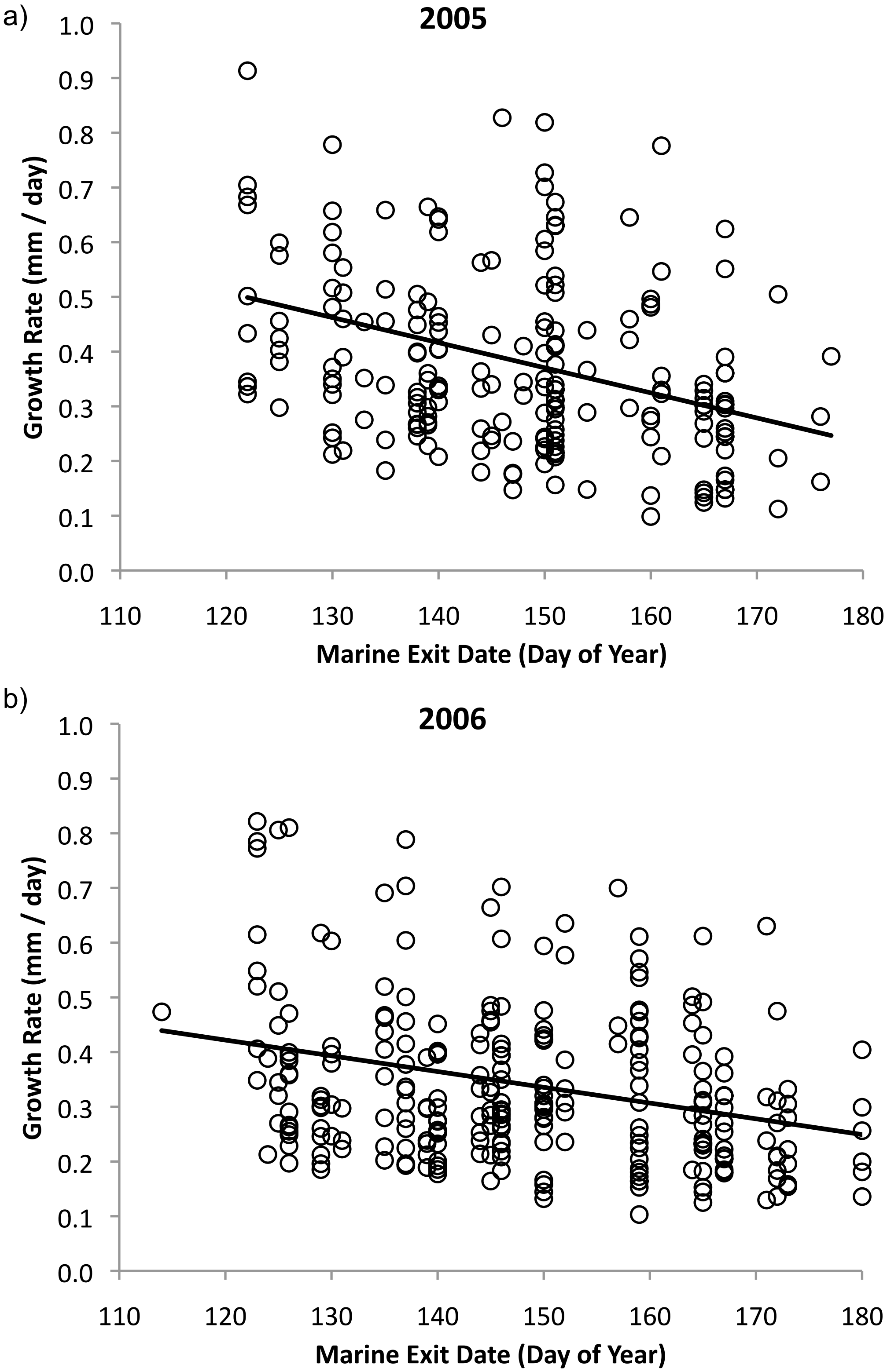


Figure 3.6 Growth rates in spring prior to marine exit for sockeye salmon returning in a) 2005 (2-factor regression: $r^2 = 0.17$, $n = 204$, date $p < 0.0001$, age $p = 0.029$) and b) 2006 (2-factor regression: $r^2 = 0.11$, $n = 263$, date $p < 0.0001$, age $p = 0.009$).

Table 3.3 Growth rates (mm / week) of maturing sockeye salmon during the spring before capture. One-way ANOVA used to test mean growth rate values of individual age-sex groups. Means connected by the same letter under significance column are not significantly different. Two-factor GLM used to test mean growth rate values by age and sex. * adjacent to p value illustrate which factor is significant.

	Age	Sex	n	Mean	±	95% C.I.	Significance	
1-factor ANOVA (Growth Rate vs Age-Sex group)								
2005	1.2	M	15	2.85	±	0.71	a	p = 0.77
	1.2	F	25	2.74	±	0.55	a	
	2.2	M	6	3.21	±	1.12	a	
	2.2	F	12	3.17	±	0.79	a	
2006	1.2	M	70	2.76	±	0.27	a	p = 0.016
	1.2	F	105	2.28	±	0.22	b	
	2.2	M	36	2.30	±	0.37	b	
	2.2	F	52	2.17	±	0.31	b	
2-factor ANOVA (Growth Rate vs Age + Sex)								
2005	1.2		40	2.78	±	0.44		p = 0.15
	2.2		18	3.18	±	0.63		
		M	21	2.95	±	0.55		p = 0.67
		F	37	2.88	±	0.48		
2006	1.2		175	2.47	±	0.18		p = 0.12
	2.2		88	2.22	±	0.20		
		M	106	2.60	±	0.25	*	p = 0.0068
		F	157	2.24	±	0.16	*	

Reproductive state of sockeye salmon varied with date of marine exit (Figure 3.7). Ovary size (dry mass) increased with later marine exit date (n = 68, $r^2 = 0.29$, $p < 0.0001$ in 2005; n = 38, $r^2 = 0.32$, p = 0.0002 in 2006). The increase in ovary mass was driven by a 5% per day increase in individual egg dry mass (n = 68, $r^2 = 0.39$, $p < 0.0001$ in 2005; n = 38, $r^2 = 0.54$, $p < 0.0001$ in 2006). In fact, fecundity decreased (Figure 3.8) by approximately 25% between May 1st and June 30th (2-factor regression: 2005 n = 68, $r^2 = 0.31$, date p = 0.0156, fork length p = 0.0002; 2006 n = 38, $r^2 = 0.43$, date p = 0.0011, fork length p = 0.0036). Male testes were larger (dry mass) for fish exiting the marine environment at later dates (n = 54, $r^2 = 0.41$, $p < 0.0001$ in 2005; n = 31, $r^2 = 0.46$, $p < 0.0001$, in 2006). The dry mass of testis was 4.4 times larger on June 30 compared to May 1 in 2005, and 3.8 times larger in 2006.

Comparisons of tissue composition between dorsal cross sections (n = 71) and complete carcasses (n = 18) were made 2006. Cross sections had slightly lower mean energy density values (8.27 vs 8.81 MJ / Kg; n = 89, $p < 0.0001$) due to lower protein composition (17.4 vs 18.7%; n = 89, p = 0.0017) while lipid composition was similar (n = 89, p = 0.108). There was a strong correlation of energy density (n = 89, p = 0.644), % lipid (n = 89, p = 0.445), % protein (n = 89, p = 0.516) and % carbon (n = 89, p = 0.885) between dorsal cross sections and complete carcasses. Dorsal cross sections were therefore considered good indicators of total body energy density and tissue composition and were used to test temporal trends in energy density and individual constituents.

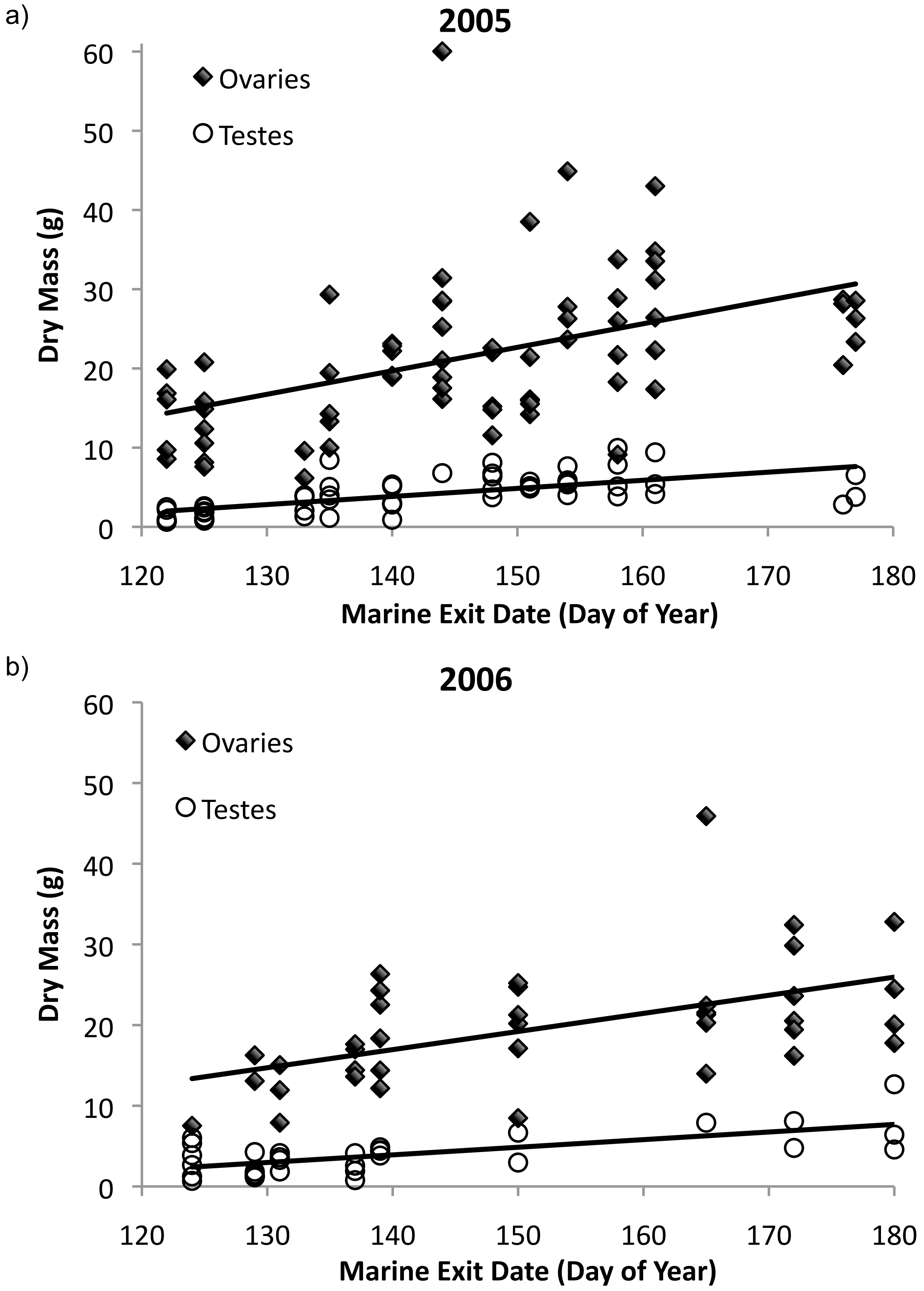
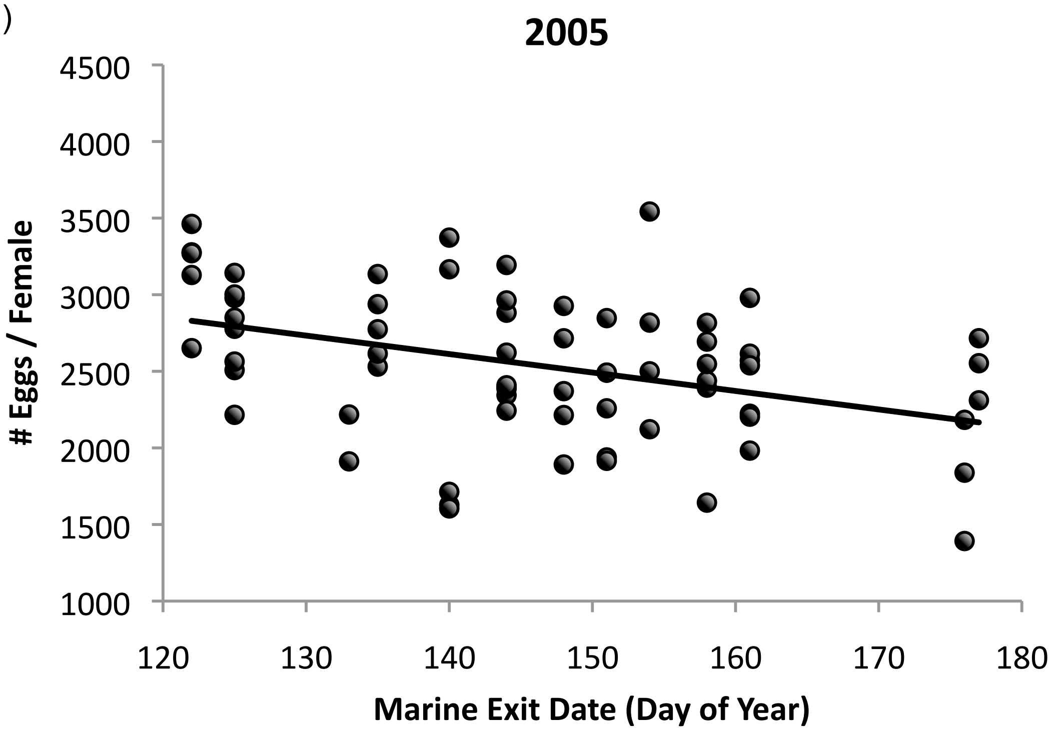


Figure 3.7 Mass of gonads at marine exit for sockeye salmon returning in a) 2005 (ovaries n = 68, $r^2 = 0.29$, $p < 0.0001$; testes n = 54, $r^2 = 0.41$, $p < 0.0001$) and b) 2006 (ovaries n = 38, $r^2 = 0.32$, $p = 0.0002$; testes n = 31, $r^2 = 0.46$, $p < 0.0001$).

a)



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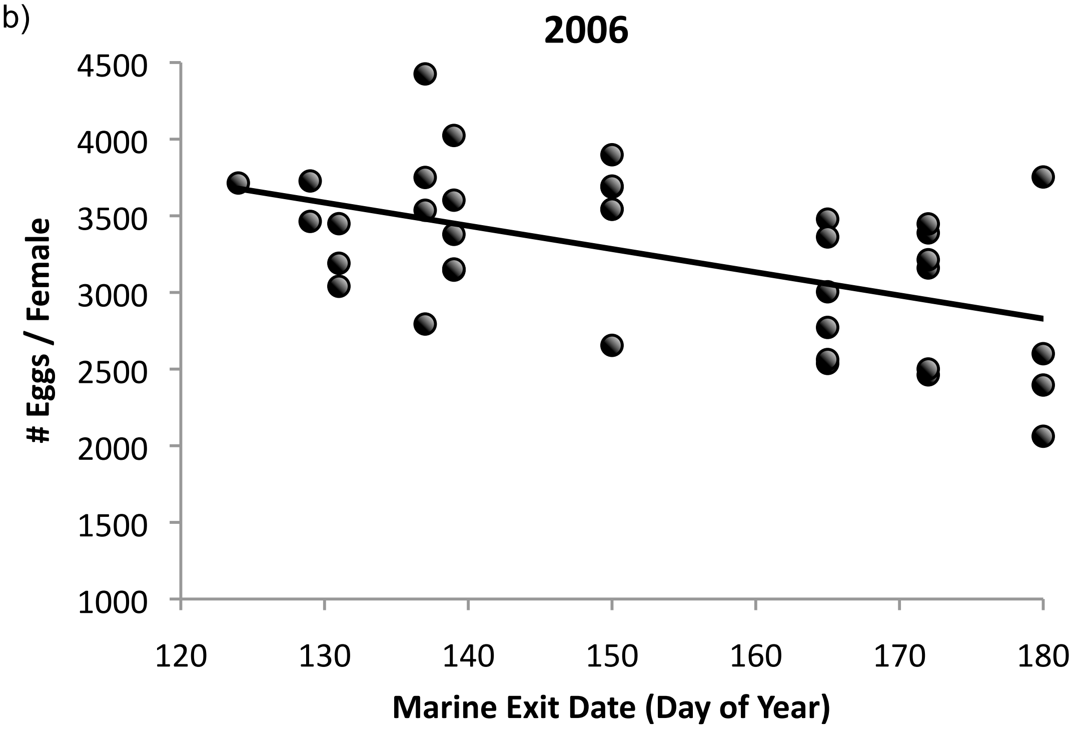

Figure 3.8 Fecundity by marine exit date for females returning in a) 2005 (2-factor regression: n = 68, r^2 = 0.31, date p = 0.0156, fork length p = 0.0002) and b) 2006 (2-factor regression: n = 38, r^2 = 0.43, date p = 0.0011, fork length p = 0.0036).

Energy density of somatic tissue from dorsal cross sections was correlated with marine exit date in both samples years (Figure 3.9). Energy density decreased with delayed marine exit date (2005 $n = 47$, $r^2 = 0.16$, $p = 0.0052$; 2006 $n = 71$, $r^2 = 0.46$, $p < 0.0001$). Variation in lipid concentration appeared to have the greatest influence on decreasing energy density associated with later marine exit date (Figure 3.10). Log transformed lipid concentration in somatic tissue was negatively correlated with delayed marine exit date ($n = 47$, $r^2 = 0.21$, $p = 0.0012$ in 2005; $n = 71$, $r^2 = 0.32$, $p < 0.0001$ in 2006). Protein and carbon concentration did not appear to be correlated with delayed marine exit day. However, these parameters were not measured directly and were therefore not tested statistically.

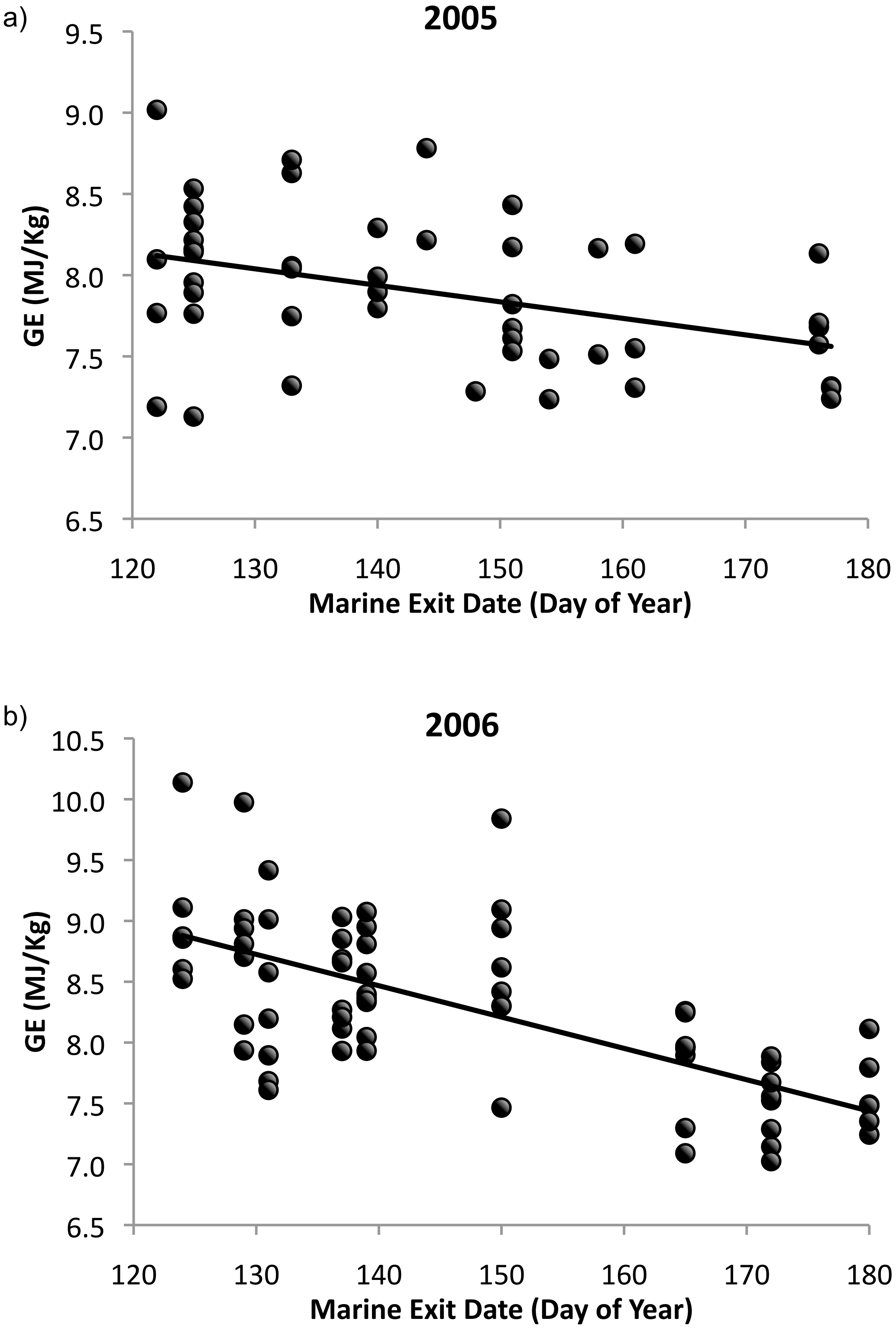

Figure 3.9 Gross somatic energy by marine exit date of sockeye salmon tissues collected in a) 2005 ($n = 47$, $r^2 = 0.16$, $p = 0.0052$) and b) 2006 ($n = 71$, $r^2 = 0.46$, $p < 0.0001$).

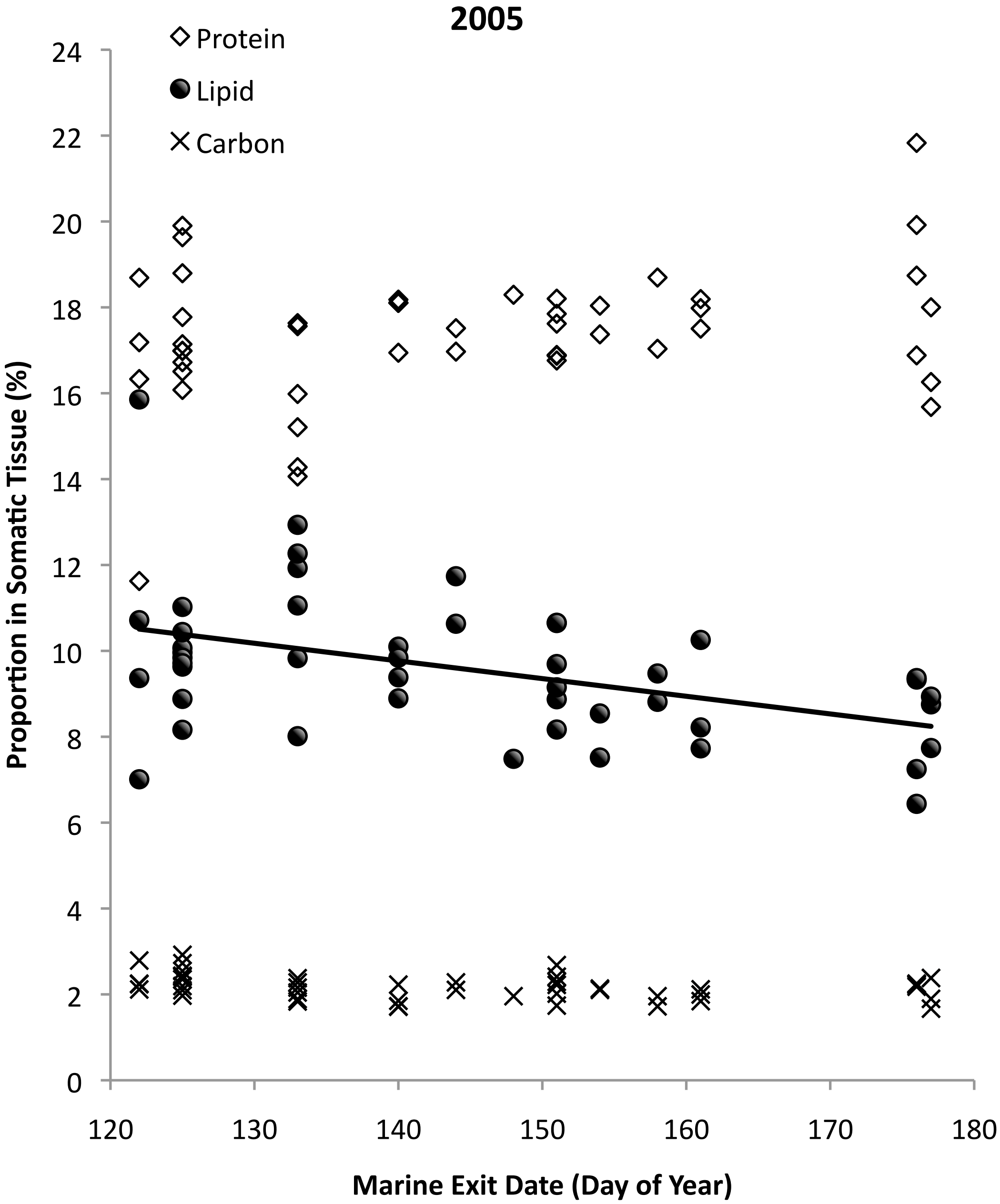

Figure 3.10 Protein, lipid and carbon composition of somatic tissues from sockeye salmon collected in 2005. Solid black line represent regression line fitted to lipid data. (log transformed lipid concentration; n = 47, r^2 = 0.21, p = 0.0012)

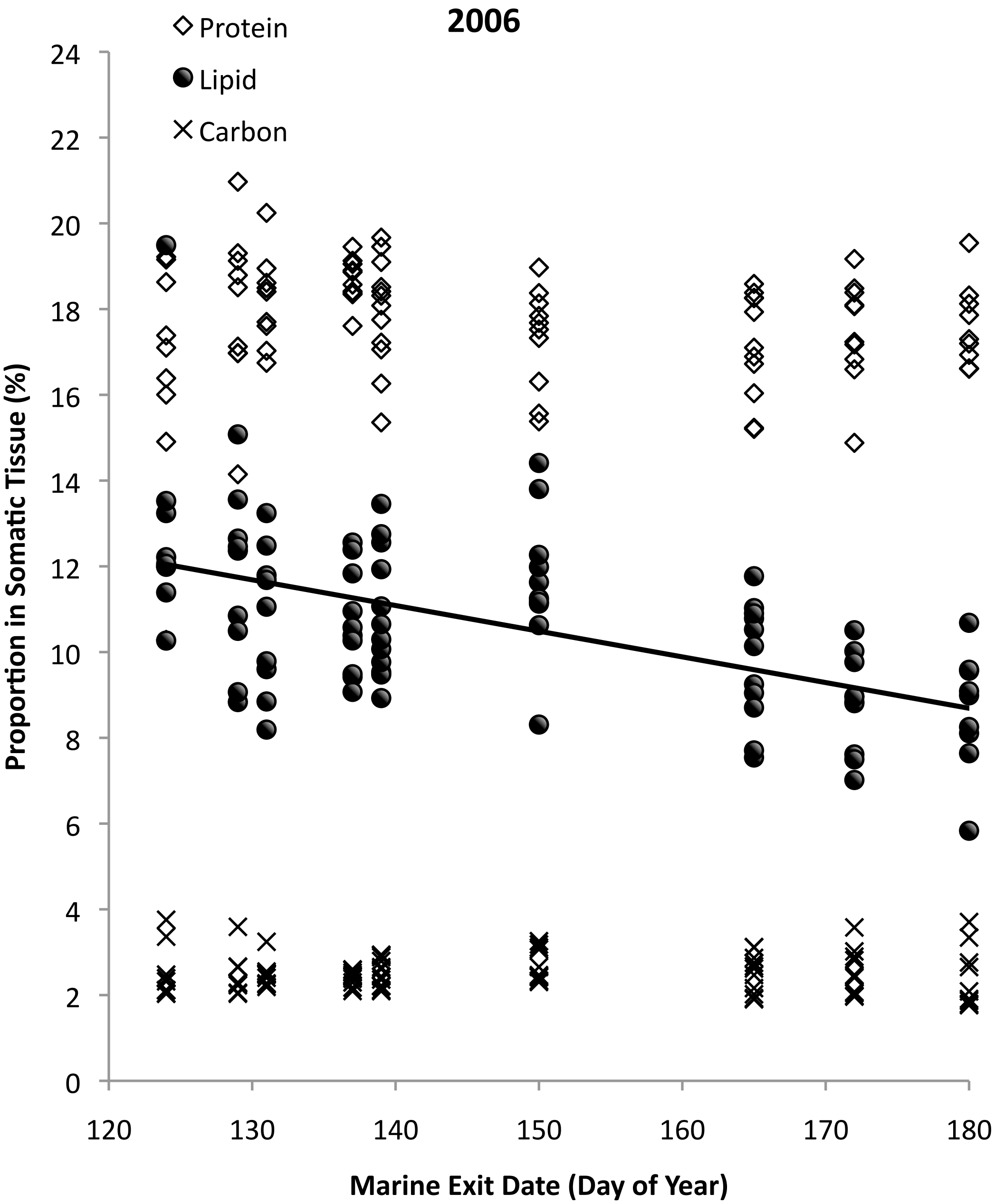

Figure 3.11 Protein, lipid and carbon composition of somatic tissues from sockeye salmon collected in 2006. Solid black line represent regression line fitted to lipid data. (log transformed lipid concentration; n = 71, r^2 = 0.32, $p < 0.0001$)

3.5 Discussion

The findings of this study are consistent with a life history model approach in explaining the individual variation of marine exit timing. In general, individuals with early marine exit were more likely to be male, were more likely to be older (2.2 vs. 1.2 age class), had higher growth rates (in the months prior to river entry), had greater somatic energy density, had smaller gonads, but (if female) had a larger number of (smaller) eggs. Despite ample variation (fork length varied by 272 mm), body size was not correlated with marine exit date. There were marginal differences in body size between sexes (males slightly larger) and age classes (2.2 aged fish slightly larger), but the temporal trends in marine exit date of the sexes (males earlier) and age classes (2.2. age class earlier) were not strong enough to overcome the background variation in body size that persisted through the migration season. These trends are visually represented in Figure 3.11.

Other studies have found body condition traits examined in this study to be correlated with marine exit timing and spawning success of fishes. Individuals that experience a higher growth rate (Brodersen et al. 2008, Kadri et al. 1995), and contain a higher energy density (Cooke et al. 2008a) tend to migrate earlier to spawning areas. This is in contrast to late-summer populations of Fraser River sockeye salmon that hold at the river mouth and delay marine exit they contain high-energy reserves resulting in greater probability of successful migration and subsequent spawning (Cooke et al. 2008a, Crossin et al. 2009, Young et al. 2006). Early migration also appears to be common

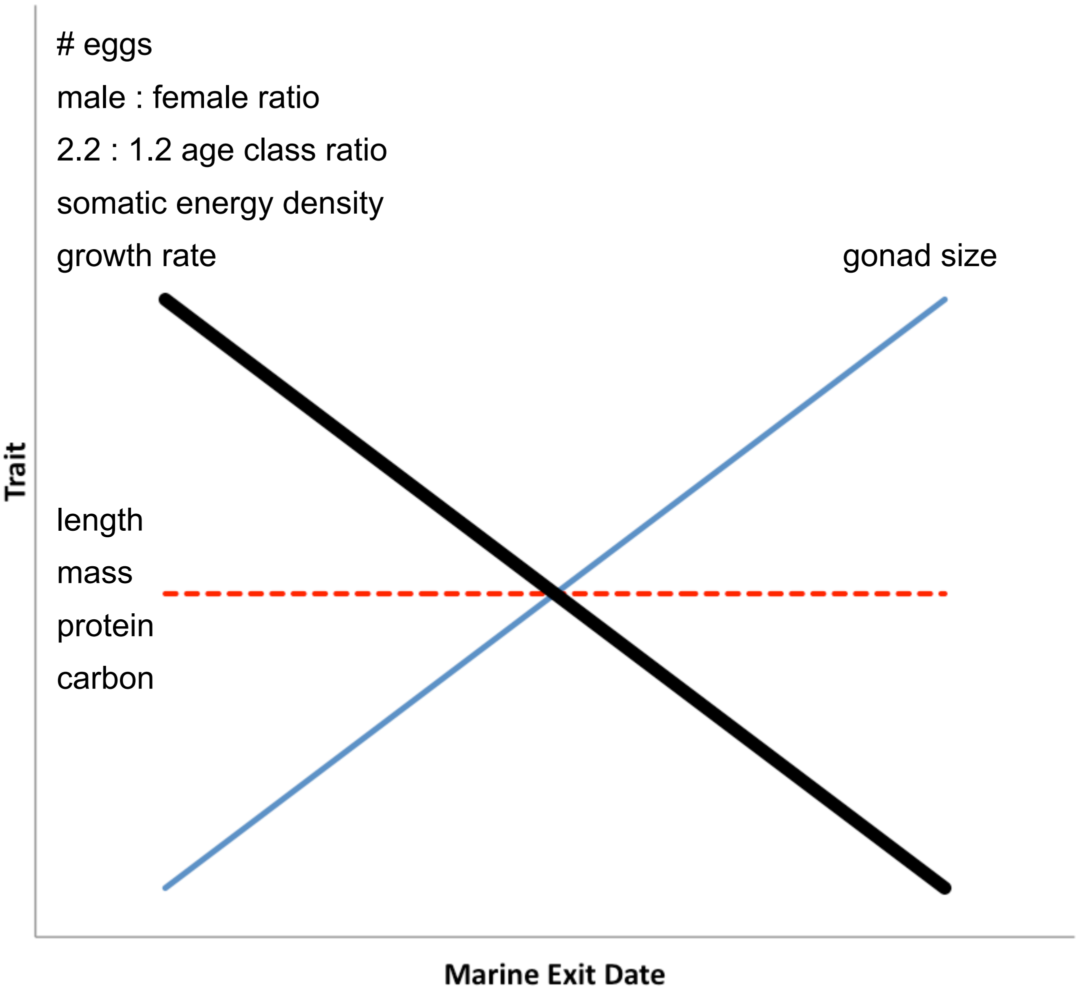

Figure 3.12 Conceptual graph of findings regarding body condition metrics and marine exit date of Copper Creek sockeye salmon.

among males (Burgner 1991, Morbey 2000, Yamamoto and Edo 2006) as well as older Pacific salmon (Molyneaux and Folletti 2005, Newell et al. 2007).

Studies that investigate salmon migration are often complicated by reproductive timing games associated with spawning (Morbey and Ydenberg 2003). The tagging data presented in Chapter 2 show that the long pre-spawning residence in Skidegate Lake (100 d or more), effectively decouples marine exit from spawning, so that early-exiting individuals did not spawn earlier. Thus, although some of the condition-dependent patterns in marine exit timing summarized in Figure 3.11 may be related to spawn timing, it seems unlikely that intrasexual spawning competition strategies are able to explain all of these patterns. I propose that a life history model in which the benefits of prolonged marine residence are weighed against the costs of freshwater migration may be able to do so.

For example, males and females differed in marine exit strategies. Considering the early migration and long wait time in the lake prior to spawning, it is unlikely that protandry associated with spawning (Morbey & Ydenberg 2003) led to the earlier marine exit of males. An alternative explanation consistent with a condition-dependent hypothesis is that total energy cost of reproduction (gonad development and reproductive behaviours) are less energetically costly for males compared to females (Hendry and Berg 1999) and therefore males can divert more resources into growth and energy reserves. This would allow males to grow faster and reach the optimal size and energetic state required for reproduction prior to females. In this study, male growth rates were greater than for females. Therefore, the marginal fitness benefit to delaying marine exit is expected to be less for males and thus lead to earlier marine exit. Crossin et al. (2009) suggested that protandrous migration of Fraser sockeye salmon was a response by males to females who are under greater developmental constraints with respect to energy, reproductive development, and subsequent reproductive behaviour.

A life history model analogous to that used to explain protandrous migration can also be used to explain the different marine exit time strategies observed between 1.2 and 2.2 age classes. In this case, the two age classes experience the same growing period at sea but different freshwater growth periods. Older fish (age 2.2) migrated to sea approximately 10 – 20% larger than their younger (age 1.2) cohorts (Figure 3.5). This size advantage for 2.2 aged individuals persists through most of their lifetime and may allow them to reach their optimal size and energetic state required for reproduction prior to the 1.2 age class. The marginal fitness benefit to delaying marine exit is therefore expected to be less for older fish.

Sockeye salmon returning to Bristol Bay are also known to eat large amounts of prey with high caloric value during the final stages of their marine migration (Nishiyama 1977). The links between energy density and growth rates to marine exit timing strategies are the foundation of life history models as they are directly linked to reproductive benefits in salmonids. The observed negative correlation between marine exit timing and energy density / growth rate in

Copper Creek sockeye salmon is explained by a basic life history trade off (Quinn 2005). Fish that have experienced good growth and high energy conditions will gain less, proportionally, after an extra week at sea than smaller fish that have experienced poor growth and low energy conditions. Differences in migration timing strategy would therefore reflect the delay of small, slow-growing fish with low energy as they grow a little more and accept some cost associated with migration after the ideal date. Alternatively, the decline in growth rate and energy status over time could be due to their catabolic state having already reduced or stopped feeding during their homeward migration at sea (Cooke et al. 2008a). In this scenario, catabolism is initiated at the onset of homeward migration regardless of location at sea such as that proposed by a displacement model. Fish arriving at a later time would therefore have a slower growth rate or lower energy status simply because they had been in a catabolic state for a longer period of time. While this alternative explanation is possible, it is unlikely, considering all the other traits correlated to marine exit that are more easily explained by a life history model.

Body size of spawning salmon has been found to be positively correlated with stream size suggesting that in small streams small body size is favoured (Beacham and Murray 1987, Lewis 1987, Quinn 2005). This likely reflects a selective optimum between the increased reproductive benefits (Burgner 1991) and increased predation costs (Quinn et al. 2003, Ruggerone et al. 2000) associated with increased body size and is likely unique to the attributes of individual streams (Quinn et al. 2001). The observation that body size did not vary with marine exit date can be explained by a life history model where by smaller fish delay their homeward migration to gain more reproductive fitness associated with greater body size. The marginal fitness benefit to delaying marine exit is expected to be greater for fish that are smaller than the optimal reproductive size required for their natal stream.

Fecundity and egg size are both important measures of reproductive success in salmonids. In this study, late-exiting sockeye salmon were more advanced (larger gonads) in their maturation process compared to early-exiting fish. Reproductive maturation likely began during migration at sea and develops according to a schedule that is influenced by photoperiod and may be independent of marine exit date (Dingle 1996). During ovary development, egg number is thought to be set months in advance of final maturation (Tyler and Sumpter 1996), while final egg size at spawning is likely determined late in the maturation process. This reflects the trade-off between the number of remaining eggs and the energetic demands of migration and reproductive maturation (Kinnison et al. 2001). While this study was unable to validate if female fecundity (number of eggs) was fixed between marine exit and spawning, the negative correlation with marine exit timing appears to be a novel discovery. This suggests that early exiting females which experience good growth and energy conditions have the potential to allocate more resources to fecundity based on their condition (Bromage et al. 1992, Jonsson et al. 1996). This phenomenon has also been found to occur in marine sun perch that delay breeding within a season to attain greater fecundity from increased growth (Schultz et al. 1991). A life history model is sufficient to explain the observed decline in fecundity associated with later marine exit of individuals from this early run sockeye salmon population.

The resources gained while feeding at sea must be partitioned between basic physiological maintenance, growth, lipid reserves, and gonads. Older and larger individuals that experience fast growth rates and reach the body size at which further increases are not worthwhile, have the advantage of being able to shift greater resources to lipid reserves important for migration and reproductive development. It is possible that some individuals work harder (take more risks) in the final weeks at sea to be able to grow enough in order to exit earlier instead of waiting. This study is consistent with other studies that have found energy reserves to be important in determining the timing and successful completion of spawning migrations in sockeye salmon populations (Cooke et al. 2008a, Cooke et al. 2006b, Crossin et al. 2009, Young et al. 2006).

Further research is required to help clarify the relationship between the condition dependence of sockeye salmon and their homeward migration. New techniques using mass spectroscopic analysis could be used to determine when and where sockeye salmon feed or cease feeding in the open Pacific. This technique is able to quantify the nitrogen ratio of specific growth rings on scales of sockeye salmon captured upon their return. As the nitrogen ratio has been found to vary geographically in open Pacific Ocean, the nitrogen ratio of individual growth rings could provide a record of when and where the feeding / growth occurs (Saino and Hattori 1987, Satterfield and Finney 2002, Welch and

Parsons 1993). While the feasibility of this method still requires investigation, comparisons of N^{15}/N^{14} ratio, in the last growth ring of returning sockeye salmon may provide useful insight to the condition dependence of marine exit. For instance a negative correlation with marine exit date would suggest that early exiting individuals were further inshore and closer to their natal stream compared to late exiting individuals when they ceased feeding and would support the displacement model. However a constant N^{15}/N^{14} ratio associated with marine exit date would suggest that feeding and subsequent growth occurred in a similar region regardless of marine exit date and would therefore support a condition-dependant migration timing hypothesis.

3.6 Conclusion

The intraspecific variation in marine exit timing of a sockeye salmon population that exhibits early marine exit and long freshwater wait time prior to spawning, appears to be a condition-dependent life history strategy. Variation in marine exit timing within a population hinges on the variation in growth and acquired energy conditions at sea prior to their homeward migration. This is in contrast to the variation of marine exit timing among different salmon populations, which experience relatively similar marine growing opportunities but different freshwater migration and spawning conditions. Marine exit timing can therefore be thought of as a population-specific adaptation to prevailing conditions within a stream that maximizes the probability of successful migration, spawning, and survival of resulting offspring.

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CHAPTER 4: GENERAL CONCLUSIONS

4.1 Thesis Summary

Migration of Pacific salmon through coastal waters to natal streams to spawn is a dominant characteristic of many north temperate marine and terrestrial ecosystems. Much of the research that examines the time that fish exit the marine environment to start their upriver migrations, has focused on the mechanistic processes that drive variation within (Cooke et al. 2008a, Cooke et al. 2006a, Crossin et al. 2009, Crossin et al. 2007, Newell 2005) and among populations (Hodgson and Quinn 2002, Hodgson et al. 2006). This thesis examined how life history decisions influence individual marine exit timing strategies within a population of sockeye salmon to (1) determine if Hodgson and Quinn's (2002) thermal avoidance hypothesis (strategy 3) is sufficient to explain the early marine exit timing and long freshwater residence times prior to spawning, and (2) determine how condition dependence influences marine exit timing strategies. My findings led me to propose an alterative hypothesis, based on a life history model, to explain the early marine exit timing and long delay before spawning of sockeye salmon returning to Copper Creek and possibly other Haida Gwaii populations.

In Chapter 2, the marine exit and spawn timing of sockeye salmon returning to Copper Creek was documented to characterize the long freshwater residence times known for this population. All spawn-timing options were available to individuals regardless of their marine exit timing strategy (marine exit date not correlated to spawning date). Also, individual spawn timing was much less variable compared to marine exit timing in the population. As a result of these two characteristics, fish that adopted an early marine exit timing strategy had much longer freshwater residence times compared to later marine exiting fish (strong negative correlation of freshwater residence time with marine exit date). I therefore suggest that marine exit and spawn timing are likely strategically independent in sockeye salmon populations that have long adult freshwater residence times and are good candidates for studying the condition dependence of marine exit timing.

The data did not support Hodgson and Quinn's (2002) thermal avoidance hypothesis (strategy 3) in explaining the early marine exit timing of sockeye salmon returning to Copper Creek. Even during mid summer the thermal regime of this stream is moderate (17-18 ^{o}C) and does not pose a risk to migrating sockeye salmon as these temperatures are below their physiological thermal thresholds.

In chapter 3, the condition dependence of marine exit timing of Copper Creek sockeye salmon was investigated. Individuals with early marine exit were more likely to be older (2.2 vs. 1.2 age class), were more likely to be male, had higher growth rates in the months prior to river entry, had greater somatic energy density, had smaller gonads, but (if female) had a larger number of (smaller) eggs. Body size, however, was not correlated with marine exit timing despite ample variation. These data support the hypothesis that marine exit timing is a condition-dependent life history strategy as a simple life history model easily explained many of the observed correlations. The variation of marine exit timing within a population is therefore suggested to hinge on the variation in growth and acquired energy conditions at sea prior to homeward migration.

Thermally based migration strategies (Hodgson and Quinn 2002) appear to be insufficient in explaining the early marine exit timing and long freshwater wait times prior to spawning of sockeye salmon returning to Copper Creek or the variation in marine exit timing among different populations on Haida Gwaii (Figure 1.1). Theories that use thermal limitations during freshwater migration are based on a trade-off between temperature driven metabolic costs and finite energy reserves for migration and reproduction (Crossin et al. 2009, Rand and Hinch 1998, Rand et al. 2006). In a basic life history framework, marine exit is an evolved strategy based on a trade-off between the fitness benefits of marine growth, the mortality costs in the ocean prior to marine exit, and by the fitness costs of upriver migration. Therefore, an alternative to energetic costs in upriver migration may be driving the cost benefit trade-off associated with the early marine exit timing and long wait times of sockeye salmon populations returning to Haida Gwaii.

There are several lines of evidence to suggest that seasonally variable predation risk may be a significant upriver migration “cost” driving the early marine exit of some sockeye populations on Haida Gwaii. Predation risk, commonly interpreted as mortality due to predation, is a function of danger, escape performance, and anti-predator behaviour as defined by Lank and

Ydenberg (2003). The following evidence illustrates how such factors can influence the potential mortality of sockeye salmon during upriver migration of Copper Creek.

First, data from Chapter 2 (Figure 2.5) clearly show that sockeye salmon returning to Copper Creek have a strong propensity to exit the marine environment and migrate upriver nocturnally. Nocturnal migrations of fishes are commonly hypothesised to be behavioural decisions or strategies to minimize predation risk by visual predators (Reebs 2002). This predator avoidance behaviour has been shown to occur in a variety of fishes and life stages such as longnose dace (*Rhinichthys cataractae*) foraging in fast flowing streams (Culp 1989), diel vertical migrations of juvenile sockeye salmon in lakes (Clark and Levy 1988, Scheuerell and Schindler 2003), seaward migration of pink, chum (Neave 1955), and Atlantic salmon smolts (Ibbotson et al. 2006). Nocturnal upriver migration therefore suggests that anti-predator behaviour may be an important consideration during upriver migration of sockeye salmon returning to Copper Creek.

Second, early marine exiting sockeye salmon populations returning to Haida Gwaii migrate up relatively small streams. Sockeye salmon have been shown to sustain substantial mortality from bear predation in smaller streams (Quinn 2005b, Quinn and Buck 2001). In fact, sockeye salmon migrating up steams on Haida Gwaii are prey to a whole host of visual predators such as Glaucous-winged Gulls (*Larus glaucescens*), Bald Eagles (*Haliaeetus leucocephalus*), river otters (*Lontra canadensis*), black bears (*Ursus* *americanus*), and even humans (*Homo sapiens*). Presumably the danger from these predators during upriver migration is highest in small, shallow streams that lack deep pools or large woody debris, which are important habitats for avoiding predation (Quinn et al. 2001). These characteristics also vary seasonally within a stream as the mean depth of the stream changes with stream discharge.

Third, the hydrological regimes of the streams on Haida Gwaii are dominated by precipitation (Figure 4.1) and are seasonally predictable. Unfortunately, seasonal discharge data from Copper Creek are unavailable. However, hydrological data are available from Pallant Creek (unpublished data from Environment Canada's Archived Hydrometric Data), an adjacent watershed of similar catchment area and lake headed stream with similar physical characteristics. The seasonal variability of stream discharge is presumably similar in Pallant Creek and Copper Creek. The striking feature of these data is that stream discharge is consistently very low during the summer months (Figure 4.2). If Copper Creek sockeye salmon exited the marine environment a few weeks prior to spawning, as in other coastal populations, they would migrate upstream during mid summer when mean stream discharge rates were the lowest and presumably predation danger was the highest. Instead, Copper Creek sockeye salmon appear to be exiting the marine environment in the spring when stream water levels are predictably higher and predation danger is subsequently lower compared to mid summer.

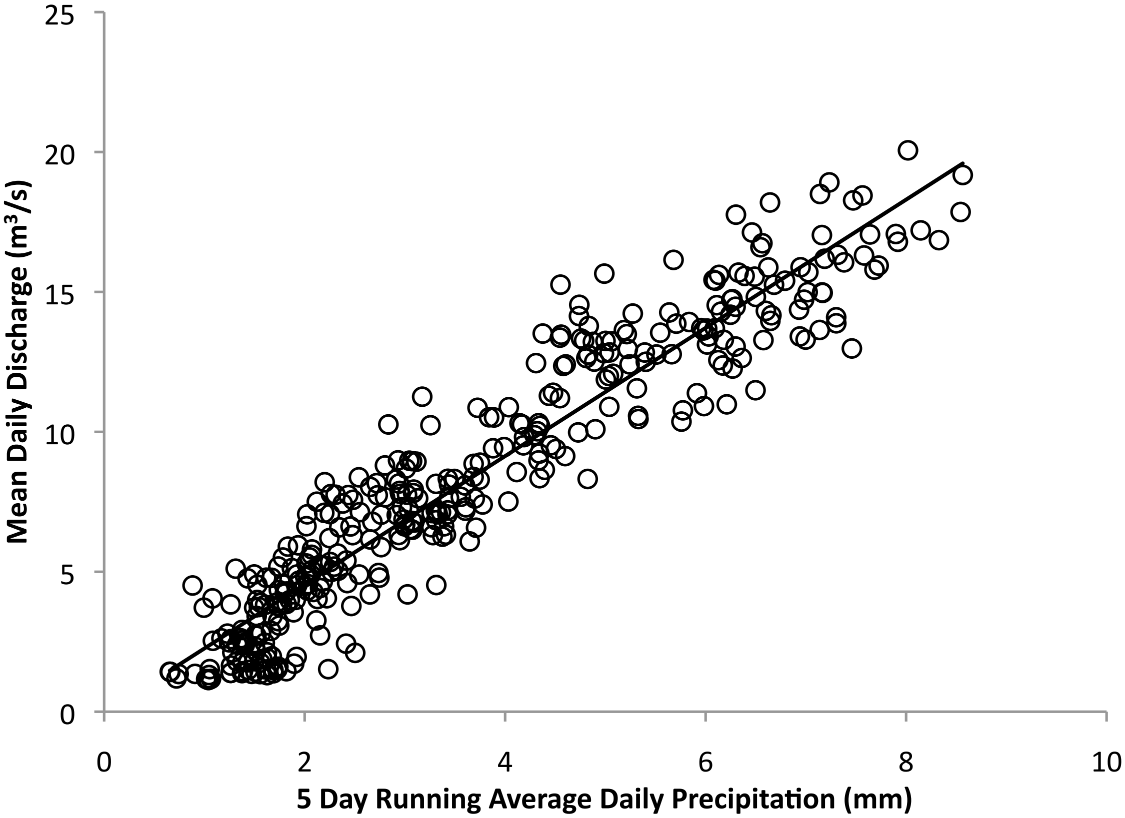

Figure 4.1 Mean daily precipitation of previous 5 days versus the mean daily discharge observed at Pallant Creek (n = 361, $r^2 = 0.90$, $p < 0.0001$), a watershed of similar catchment area and lake headed stream with similar physical characteristics to Copper Creek. (unpublished data from Environment Canada's National Climate Data and Information Archive and Archived Hydrometric Data).

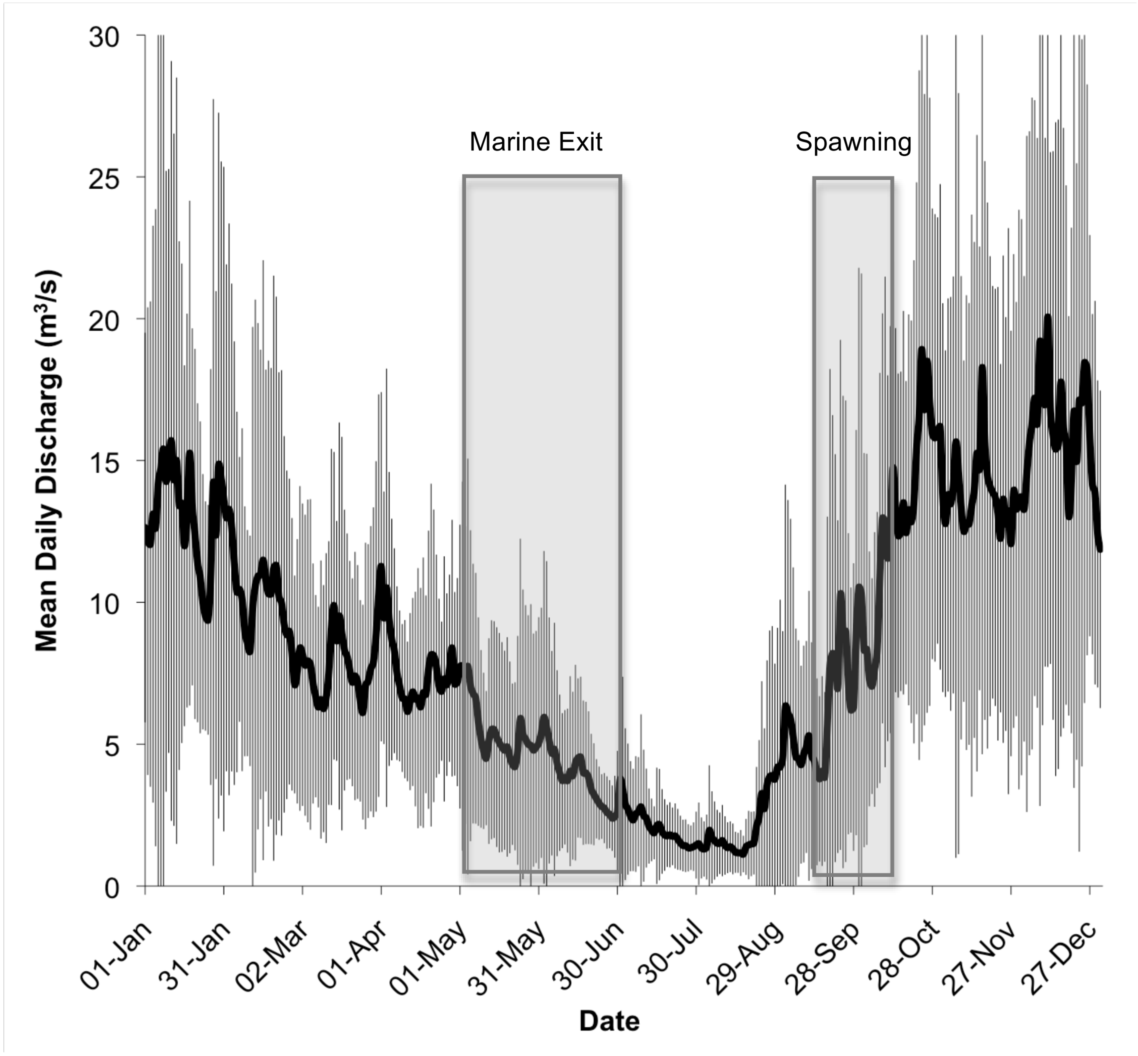

Figure 4.2 Mean daily discharge at Pallant Creek between 1985 and 2005. Vertical bars along the mean daily discharge represent one standard deviation. Transparent grey boxes represent the timing of Copper Creek sockeye salmon marine exit and spawning. Note the low variability and low mean daily discharge during the summer months prior to spawning.

In light of this evidence, I propose that anti-predator behaviour may be driving early marine exit of some sockeye salmon populations. Modifying the basic life history model used in this thesis to reflect this hypothesis, marine exit is viewed as an evolved life history decision influenced by (a) the benefits of marine growth opportunities, (b) mortality costs in the ocean in the period prior to spawning, and (c) by the energetic costs and predation risk of upriver migration. This hypothesis not only applies to comparisons of individuals within populations but also comparisons among different populations. For instance, in the context of how predation risk influences individual marine exit strategies within a population, marine exit may be conditionally dependant. This would reflect a life history trade-off where fish in “better” condition are able to allocate more resources to anti-predator behaviour by exiting earlier. The variation of marine exit strategies among different populations likely reflects the variation of in-river migration costs between river systems due to predation. Energetic costs are likely a more significant component of upriver migration cost in large rivers where upriver migrations are energetically expensive due to long migration distances, high river flows, or high water temperatures such as populations returning to the Fraser River. This is in contrast to sockeye salmon populations on Haida Gwaii that return to small cool river systems with short easy migrations where predation risk is likely a more significant determinant of upriver migration cost. This does not suggest that mortality due to predation is necessarily high for sockeye salmon returning to Copper Creek. Instead mortality would likely be higher if fish migrated upriver at a different time, such as the middle of summer when river flows are low and predation danger was greater.

In-stream predation has generally not been viewed as a selective factor on run timing (Quinn 2005). This may be an artifact of available research, a significant proportion of which has been conducted on large rivers where predation may be less important. While many studies focus on the physiological or mechanistic limitations (e.g. temperature) of marine exit timing and river migration, few address how behavioural strategies can act as selective agents specifically on run timing of salmonids. While some examples exist, these studies use a life history framework to examine the behavioural strategies during spawning (Carlson et al. 2004, Morbey 2000, Morbey and Ydenberg 2003, Snover et al. 2006). While the study of predation risk has proven problematic (Lank and Ydenberg 2003), further study with respect to how salmon respond to predation risk during river migrations may shed light on the variation in marine exit observed in pacific salmon, especially in populations returning to smaller streams.

4.2 Conclusion

In conclusion, I found support for the hypothesis that marine exit timing within a population is likely condition dependent as marine exit strategy varies between age classes, between males and females, between fish with high and low energy reserves, and between fast and slow growing fish. The variation in marine exit timing and delay prior to spawning (freshwater residence time) among populations is likely the result of variable upriver migration costs between different streams. In the case of small coastal sockeye salmon populations with short easy migration such as Copper Creek on Haida Gwaii, early marine exit and long delays prior to spawning may be an adapted migration strategy to reduce the predation mortality associated with upriver migration.

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