ENERGY EXPENDITURE DURING BREEDING COMPETITION BETWEEN FERAL CHINOOK SALMON (*Oncorhynchus tshawytscha*) AND NATIVE ATLANTIC SALMON (*Salmo salar*)

by

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Abstract

The introduction of non-native species to many parts of the world is increasing and continues to be a major concern amongst scientists. My objective was to examine competition for space and other resources between native and introduced salmonids. Through physiological telemetry and behavioural observation, the movements, energy expenditure, and interactions within and between spawning feral Chinook salmon and released native Atlantic salmon were measured in Bronte Creek, a tributary of Lake Ontario. By combining telemetry and visual observations, the frequency, duration, and energy cost of all behaviours (including routine behaviours) were determined. The data were used to construct an energy budget for each species, to identify additional energy costs due to interspecific interactions, and the degree to which the added cost may influence reproductive success for both species. Chinook salmon were observed to be dominant to Atlantic salmon on the spawning grounds and had the highest average daily energy expenditure, 7090 cal/kg/day. Atlantic salmon spent most of their time hiding under rocks or holding in areas where Chinook salmon were not present and females had an average daily energy expenditure of 2703 cal/kg/day. Male Atlantic salmon consumed more energy on average per day than did female Atlantic salmon, 3771 cal/kg/day. However, Atlantic salmon remained on the spawning grounds for a greater amount of time and so were observed to conserve energy. If the frequency of interactive behaviours between the species were to increase then spawning may be compromised in that less energy may then be available for reproductive success. Neither of the species were seen to spawn in this study. This may be related to the additional energy costs of interspecific competition or to the presence of an introduced species on the spawning grounds of a native fish species. Results of this study may also be applicable to potential interactions between native Chinook salmon and farmed Atlantic salmon in British Columbia.

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1.0 Introduction

Commercial, marine, fin-fish aquaculture in Canada represents a growing industry and this has been the case only since the early 1970's (Volpe *et al.* 2001). In this respect, salmon culture is a relatively new science and research is required to ensure that aquaculture is an environmentally sustainable industry. One such study includes the identifying of interactions between wild and cultured salmonids.

Salmon species, including Atlantic salmon, chinook salmon, and coho salmon are farmed extensively along the coasts of Vancouver Island in British Columbia (BC) (McKinnell 1997). Most of this farming includes the use of floating sea-pen systems, where the fish grow in 100m x 100m net cages in an open ocean environment. Atlantic salmon presently represent 80% of the total production in the aquaculture industry in BC (Volpe *et al.* 2001). The rearing of Atlantic salmon in British Columbia and Washington State has caused heated debates among those in the industry, fishermen, environmental groups, and government authorities concerning the potential ecological effects of introducing Atlantic salmon to the Pacific coast. From 1987 to 1998, a total of 236,974 Atlantic salmon were reported to have escaped from fish farms surrounding Vancouver Island (Volpe *et al.* 2001). Farmed Atlantic salmon have been observed migrating into coastal rivers and successful spawning has been documented in several rivers on Vancouver Island (Volpe *et al.* 2000), in New Brunswick (Carr *et al.* 1997), in Norway (Lura and Saegrov (1991), and in Scotland (Webb *et al.* 1991). The potential for escaped Atlantic salmon to compete with native Pacific salmon species for food, habitat, and spawning territory is poorly understood. Therefore, it is essential to study the ecological effects of Atlantic salmon that escape into the wild, including competition with native species.

Competition occurs when two organisms require the same resource, which may or may

not be in limited supply. Competition within and between species may result in ecological shifts (Crawford 2001). Other trophic levels within the food web may be affected and consequent changes in the ecosystem may result. Interspecific competition between introduced and native species is difficult to measure due to the complexity of the natural world, however invasive introduced organisms may represent potential ecological threats (Mayer *et al.* 2000). For example, the zebra mussel (*Dreissena polymorpha*) was introduced to the Laurentian Great Lakes in 1986 and since this time water clarity has increased and several species of phytoplankton have been eliminated from Lake Erie due to filter feeding by mussels (Zorpette 1996; Mayer *et al.* 2000). This, in turn, has negatively affected the population of competing zooplankton. Yellow Perch have decreased in numbers and this has been attributed to competition for food and to an increase in light levels due to high zebra mussel concentrations (Mayer *et al.* 2000). Zebra mussels are an example of an invasive species that may have caused competitive exclusion of native species through competition for a food resource. By studying the interactions between species, effects of introduced species on ecosystems and food webs may continue to be identified.

Interactions within and between fish species include specific behaviours of the individual fish that may result from competition for food or space. Each of these behaviours represent an energy cost to the individual fish. Both Pacific and Atlantic salmon species do not eat during spawning migrations or during reproduction (Jonsson *et al.* 1991; Geist *et al.* 2000). Therefore, the fish rely completely on energy reserves to reproduce. Pacific salmon, being semelparous, rely on their energy reserves for migration up a river to their natal spawning grounds, for reproduction and for a short time post-spawning until their death (Healey 1991; Geist *et al.* 2000). Atlantic salmon, being iteroparous, must use energy reserves to migrate upstream to the spawning grounds, reproduce, and then migrate downstream to return to the ocean (Jonsson *et al.*

1991). Because the fish must rely on energy reserves alone, the spawning grounds provide an excellent place to study energy partitioning by fish species.

Trade-offs exist regarding energy use on the spawning grounds. If energy is used for specific behaviours (Healey *et al.* 2003), for competition with other species, or for extensive movements around physical barriers (Hinch *et al* 1996), then less energy will be available for actual spawning activity and reproductive success may be compromised. In this respect, measuring how fish partition available energy among ecophysiological activities such as growth, predation, reproduction, and competition will contribute to our understanding of the long term consequences of competition between fish species on the spawning grounds (Healey *et al.* 2003).

Few studies have been done on energy allocation in free-living animals (Cooke *et al.* 2000; Healey *et al.* 2003). The purpose of this thesis was to measure energy budgets, including the energy cost of competition, between adult Atlantic salmon and Chinook salmon on the spawning grounds of Bronte Creek, Ontario. Electromyogram telemetry was used in conjunction with visual observations and stream survey measurements to monitor movements, habitat use, spawning behaviour and energy expenditure of individuals. Relationships between EMG tag signals, swimming speed and energy expenditure have been published for Chinook salmon (Geist *et al.* 2000) and I used these relationships to convert field EMG data into energy expenditure. Published relationships for EMG tag signals, oxygen consumption, and energy expenditure for Atlantic salmon are limited, so I conducted a series of swim tunnel measurements to develop the relationships for this species. The field and laboratory data were used to calculate energy budgets, energy partitioning, patterns of behavioural interaction, and costs associated with habitat use and intra and interspecies interactions. Simply, my hypothesis is that there will indeed be interactions within and between the species and that Chinook salmon will dominate because of their size and undomesticated nature, even though the Atlantic salmon

will have primary residency. Successful spawning of Chinook salmon has been observed in Bronte Creek in previous years, and it is anticipated that the Atlantic salmon will also spawn, probably after the Chinook salmon have completed spawning.

In Bronte Creek, Atlantic salmon are a native species, but were extirpated in the early 20th century (Crawford 2001; Scott *et al.* 2003). Chinook salmon are stocked every year in the creek as part of a government program to increase fish population numbers for the sport fishery (Crawford 2001). Bronte Creek is a model system of interactions between native and alien salmonids where Atlantic salmon are native and Chinook salmon are feral. In British Columbia, Atlantic salmon is the alien species which may compete with native Pacific salmon including Chinook. Although the results from Bronte Creek may not be directly transferable, they are still relevant to understanding the competitive relationships between these species.

1.1 Electromyogram Telemetry

Telemetry involves the tracking of a tagged animal and the technique is used extensively in field ecology. Radio telemetry has been used since it was first introduced in the 1950's (Trefethen 1956) and involves a simple transmitter attached to the animal that transmits a "chirp" and allows a technician with a directional antenna to locate and track the tagged animal in its natural environment. In the 1970's, physiological telemetry was developed in which the radio tag is capable of monitoring and transmitting information about physiological state (eg. body temperature, heart rate, muscle electrical activity) (Priede 1978; Kaseloo *et al.* 1992).

Electromyogram (EMG) telemetry, which involves the remote measurement of muscular electrical activity as a means to evaluate activity levels and energy level in free living animals has been the focus of many studies in the last 2 decades (eg. Weatherley *et al.* 1982; Kaseloo *et al.* 1992; McKinley and Power 1992; Hinch *et al.* 1996; Healey *et al.* 2003).

EMG technology has substantially improved throughout this time (Beddow and McKinley 1998). EMGs are bioelectrical discharges that are strongly correlated with the degree and duration of muscle tension in fish species (Kaseloo *et al.* 1992; Okland *et al.* 2000). As a muscle contracts, an EMG is generated by each individual myomere and electrical impulses are distributed along the axial musculature of the fish. These electrical impulses can be measured and transmitted using telemetry devices (Beddow and McKinley 1998).

EMG telemetry can be used to provide a quantitative indication of fish activity and, in conjunction with swim speed and oxygen consumption measurements, can be used to obtain estimates of the metabolic cost of activity (Weatherley *et al.* 1982; McKinley and Power 1992; Okland *et al.* 1997; Cooke *et al.* 2000). Several studies have used EMG telemetry to estimate energy costs of specific behaviours and movements of fish in the wild including sockeye salmon (Hinch *et al.* 1996; Healey *et al.* 2003; Standen 2001). EMG telemetry has also been used to estimate energy use during forced swimming in swim tunnels (Okland *et al.* 1997; Beddow and McKinley 1998; Geist *et al.* 2000). Other studies have used EMG telemetry to monitor energy expenditure of fish living in tanks that simulate natural conditions in an attempt to estimate energy use of the fish in its natural habitat (Cooke *et al.* 2000; Okland *et al.* 2000; Thorstad *et al.* 2000).

1.2 Atlantic Salmon (*Salmo salar*)

In Canada, Atlantic salmon are native on the east coast from the Arctic Circle south to Quebec and Nova Scotia and the St. Lawrence basin, including Lake Ontario. Atlantic salmon originally occurred in the rivers of every country with borders on the North Atlantic Ocean and the Baltic Sea, as well as Czechoslovakia, Luxembourg, and Switzerland (Mills 1989). Populations of salmon have decreased throughout their range and they are presently completely extirpated from many rivers due to construction of navigation locks and dams and to overfishing and pollution (Mills 1989).

Individuals have been reported to be up to 1.3 m long and weighing 35.9 kg, but most wild fish are smaller (Mills 1989). In the marine environment Atlantic salmon appear brownish above, with silver sides and they are the only salmonid to have large black spots on the operculum. During spawning in freshwater, the males develop a curved lower jaw, a kype, and their colour becomes greenish (Okland *et al.* 1995). Atlantic salmon are farmed on both coasts of Canada (Mills 1989). The species represents the largest production in aquaculture in Canada due to the fact that Atlantic salmon grow well in high densities in captivity, eat manufactured feed readily, and are reasonably disease resistant (BC Environmental Assessment Office 1997).

Atlantic salmon may complete several spawning cycles before they die, although mortality rates after spawning are high. Mature Atlantic salmon return to their natal rivers, after six months to four years at sea, at various times of the year, starting in late July (Mills 1989) and spawn in the autumn and winter (Jonsson *et al.* 1991). On approaching freshwater the fish cease feeding. After spawning the surviving kelts return to sea and resume feeding (Mills 1989).

Atlantic salmon prefer silt-free gravel for spawning and redds are usually found from the upper reaches of the river down to the tidal level (Mills 1989). Redds are usually seen in riffles

or in faster flowing water at the head and tail of pools, as Atlantic salmon prefer gravel that is well aerated. The greatest proportion of redds are seen in the upper reaches of rivers and tributaries as the flow is more turbulent in these areas (Mills 1989). Redds are usually constructed in gravel and stones with approximate size 2.5 to 15.3 cm in diameter, and are most often seen in rivers where the gradient is about 3% (Mills 1989) and a water velocity of 93+/-6 cm/s is preferred (Okland *et al.* 1995). After spawning most of the males die and a small proportion of the females return to the sea (Mills 1989; Jonsson *et al.* 1991).

The eggs hatch in late March to early April and alevins emerge from the gravel as fry after the yolk is absorbed, 3 to 5 weeks later (Mills 1989). After one year in freshwater nurseries the fry develop into parr. Parr remain in freshwater until the spring of their second, third, or fourth year, feeding on aquatic insects and then turn silver and migrate to sea from April to June as smolts (Mills 1989). The progeny of one fish may not all go to sea in the same year or return at the same time (Mills 1989). Atlantic salmon travel great distances offshore during their ocean life and large feeding grounds have been identified off the coast of Greenland. They mainly feed on amphipods, euphausids, herring, capelin, and young cod in the Atlantic Ocean, but are opportunistic feeders and so will prey on what they can find (Mills 1989; Hansen and Quinn 1998).

1.3 Chinook Salmon (*Oncorhynchus tshawytscha*)

Chinook salmon are native on the west coast of North America from the Berring Strait, south to Southern California. Population numbers of Chinook salmon have decreased substantially over the last century throughout its entire native range, mainly due to habitat destruction (Noakes *et al.* 2000; Crawford 2001).

Game fish have been caught up to 1.6 m long and weighing 57.2 kg (Crawford 2001). In the marine environment the fish are greenish-blue, black above, and silver to white below. They are characterized amongst salmonids by having small black spots on both lobes of the caudal fin and a black pigment along the base of the teeth (Healey 1991). In the freshwater, during the spawning season, the fish appear very dark and males develop a kype. In Canada, they are farmed on the west coast of British Columbia. Chinook salmon have also been introduced extensively, including in the Great Lakes, in an effort to enhance the sport fishery (Crawford 2001; Ontario Ministry of Natural Resources 2001).

In British Columbia there are 2 wild types of Chinook salmon: both are anadromous and semelparous (Healey 2001). The most common form is the ocean-type Chinook, which emerge from the gravel in the spring, migrate to sea during the following 3 months and spend their ocean years in coastal waters (Healey 2001). They return in the early fall a few days to weeks prior to spawning. The second form is the stream-type Chinook which emerge in the spring and spend one year in freshwater before migrating to the sea (Healey 2001). These fish usually migrate far offshore. The stream-type Chinook return to their natal river several months before spawning and spawn in the headwater tributaries of large rivers, while Ocean-type chinook spawn near tidewaters (Healey 2001). Ocean-type Chinook may spend up to seven years at sea and stream-type chinook may spend up to eight years at sea and all fish die after spawning once (Healey 1991).

The timing of the Chinook return migration to natal rivers depends to a large extent on location of the river and Chinook salmon may be seen to return for spawning during any month of the year. However, runs usually occur between May and October on the west coast of Canada (Healey 1991) and into early November in the Great Lakes (Crawford 1991). Peaks in the runs, again are dependent on the location of the river, but usually occur in June, August and/or

October. Chinook populations in northern rivers tend to return earlier than those of more southern rivers (Healey 1991). Thus, Chinook in more northern rivers tend to spawn earlier than the southern populations, but most spawning is seen between July and January. There may also be a difference in return migration times within a single river, however early run fish tend to delay spawning and spawn with the later run fish in the fall (Healey 1991). All Chinook salmon cease feeding upon starting their freshwater spawning migration.

There appears to be much variability in the characteristics of Chinook salmon spawning habitat. Chinook salmon have been seen to spawn in water depths from a few centimetres to several meters and may spawn in the main stem of rivers or in smaller tributaries (Healey 1991). Water velocities may range from 10 to 150 cm/s in locations where redds are found and Chinook salmon seem to prefer coarse gravel with a few large cobbles. The eggs in the redd may be buried 20 to 36 cm deep in some areas and 10 to 80 cm deep in other areas. Chinook salmon prefer high water velocities and redds are typically found at the heads of riffles and downstream of log jams (Healey 1991).

Chinook salmon fry emerge in the spring and begin downstream migrations to the ocean from March to June (Healey 1991). The stream-type Chinook remain in a freshwater nursery for one year and then migrate downstream to the ocean. Once the fish reach the ocean, the ocean-type Chinook do not usually migrate further than 1,000 km from their natal stream, but the stream-type Chinook salmon migrate far offshore and have been captured by commercial fishing fleets off the coast of southeast Alaska and in the Berring Sea (Healey 1991). Immature Chinook salmon may also migrate south of their natal streams (Healey 1991). Herring, pelagic amphipods, adult insects, crustacean larvae and sometimes squid have all been found in the stomachs of Chinook salmon.

There are many similarities between the timing of migrations, the location of redds, and the characteristics of spawning habitats of Atlantic salmon and Chinook, especially stream-type Chinook salmon (Hansen and Quinn 1998). Both species return to spawn to their natal rivers at various times of the year, but peak runs are seen in the fall for both groups of fish. In some areas, Atlantic salmon may return to the natal river earlier than the Chinook salmon, but it appears as though both species may still spawn at the same time from late fall until early winter. Both species have also been seen to spawn into January (Hansen and Quinn 1998). Both Atlantic and Chinook salmon prefer high water velocities, and redds for both species are found at the head of riffles and in the headwaters of rivers. The preferred spawning substrate for each species is similar with medium-sized gravel and a few large cobbles (Hansen and Quinn 1998). The similarity in spawning habitat and time of spawning for Chinook and Atlantic salmon suggests the potential for competition between the species for spawning habitat. This study was designed to measure the intensity and the cost in energetic terms of such competition.

2.0 Methods

2.1 Field Study

Bronte Creek was chosen as the study site because it historically supported Atlantic salmon, currently supports a run of feral Chinook salmon, and is of a size and flow regime that permits tracking and observation of EMG tagged salmon. During the late summer and early fall of 2002, Bronte Creek (Lat:43.3N, Lng: 79.72W) was surveyed, from the mouth, upstream to a series of dams (Figure 1), which prevent passage of fish species. Spawning grounds were identified in Lowville Park (Figure 2) based on substrate (John Fitzsimons, Department of Fisheries and Oceans Canada, *pers.comm.*, June 12, 2002). Flagging tape was tied to trees every 100m along a 1.5km stretch of spawning grounds to create physical reference locations for fish observations. In the fall and winter of 2002, water and air temperatures, dissolved oxygen, water velocity, and water levels (measuring stick anchored 10m upstream of main corner pool) were all recorded from the same location on the spawning grounds of Bronte Creek. As well, water samples were taken from the same location in the creek in early September and late November. These samples were analyzed for phosphate, nitrate, total dissolved solids, alkalinity, pH, and *E. coli* by Chemisar Laboratories in Guelph, Ontario.

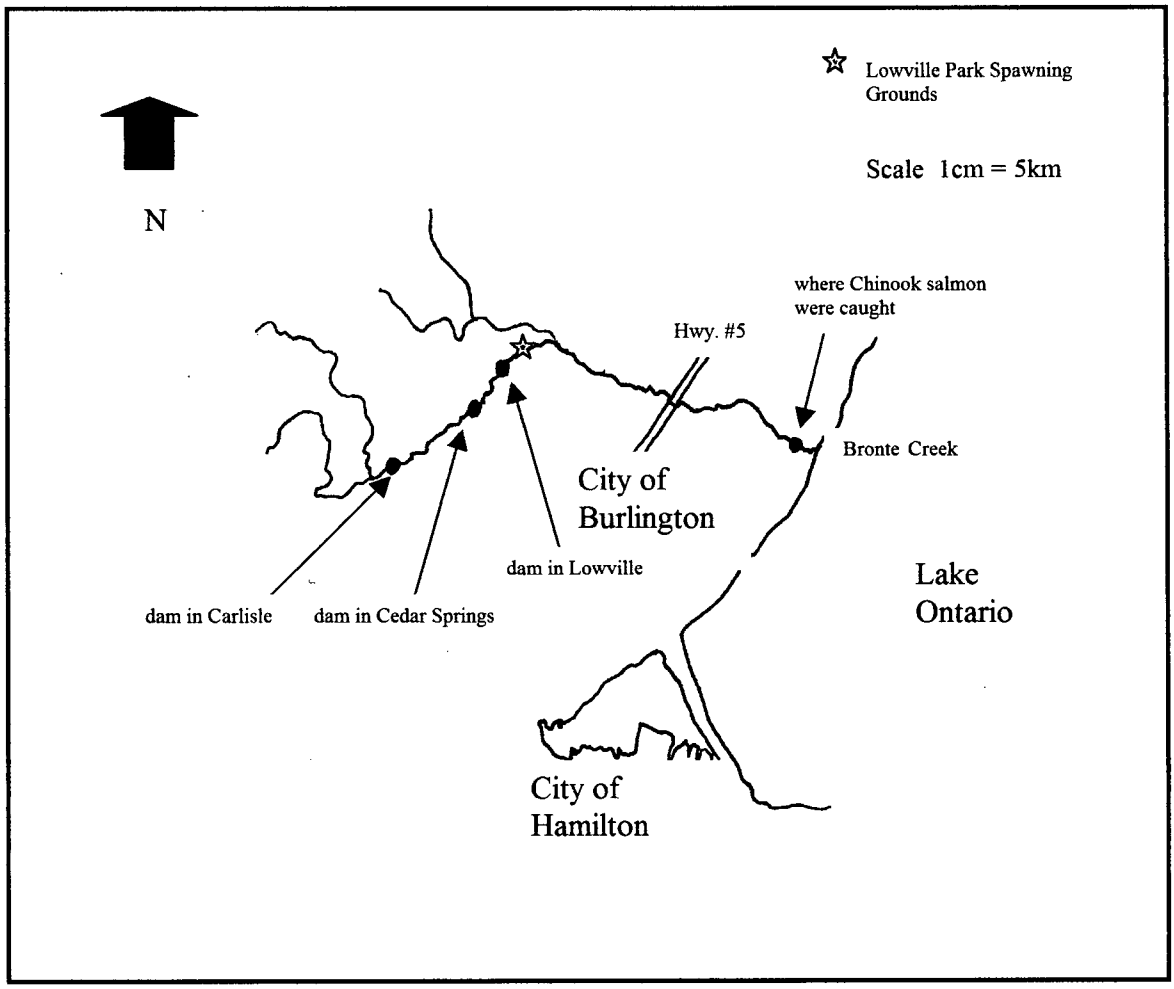

Figure 1: Map of Bronte Creek showing spawning grounds, dams, and relevant reference points in Ontario.

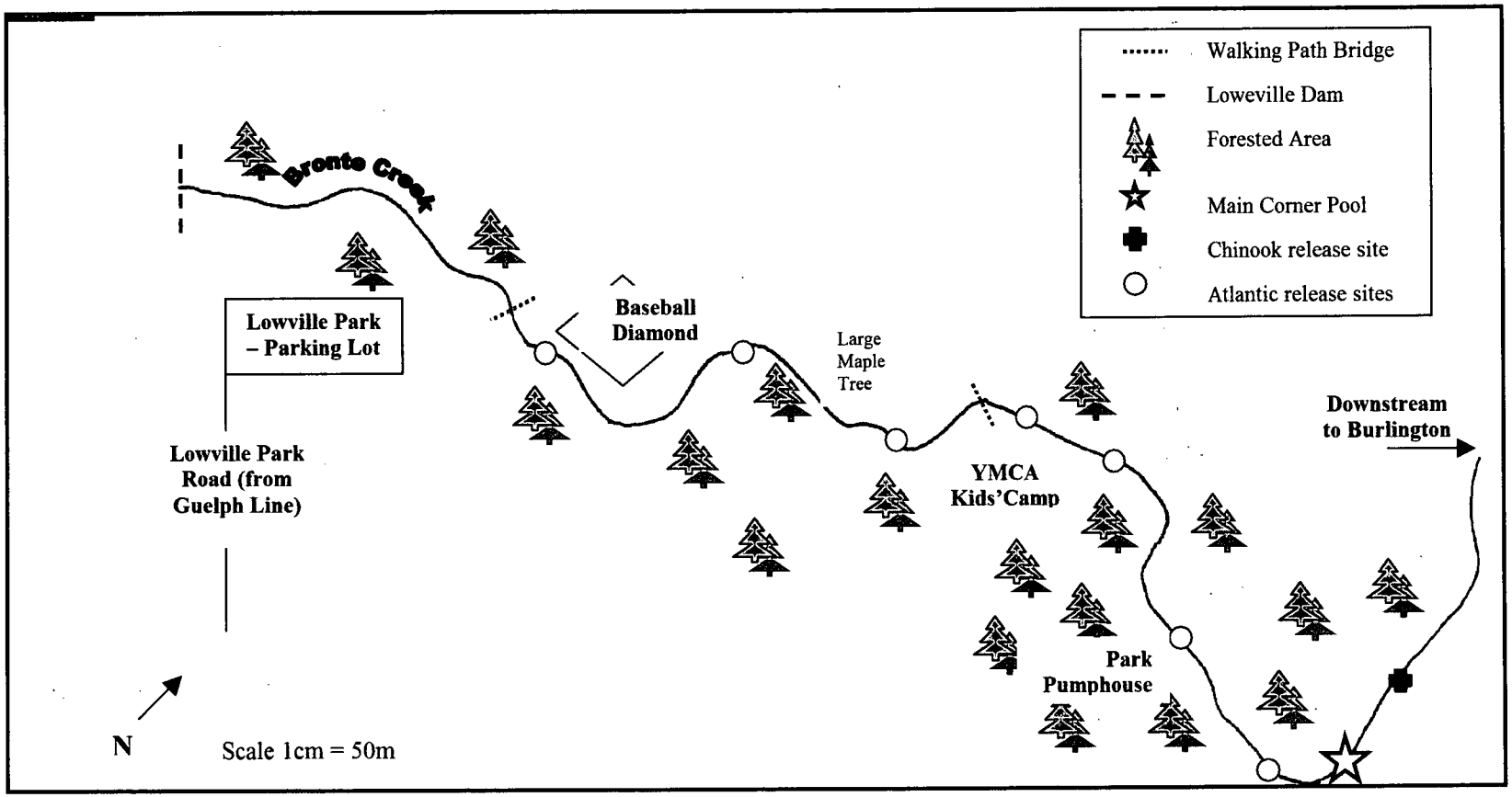

Figure 2: The spawning grounds of Lowville Park, Lowville, Ontario. Access to the park is from Lowville Park Road, off of Hwy 1 or the Guelph Line, Lowville.

Fish and Transport

Atlantic salmon used for the Bronte Creek study were hatchery reared, 4-5 year old, adults approaching maturity. They were 2-4 kg in size and from the Ontario Ministry of Natural Resources (OMNR) Fish Research Station in Codrington. The fish had been maintained in freshwater throughout their lives. Five males and five females were tagged with EMG transmitters and Floy tags and allowed to recover in tanks at the Codrington hatchery for two weeks. Ten additional Atlantic salmon were tagged with radio transmitters pushed down the esophagus into the stomach (see Surgical Technique below). On October 10, prior to the arrival of any Chinook salmon, the 20 Atlantic salmon were transported to Lowville Park and released into the creek at various locations along a 900 m stretch of the spawning grounds. Between October 13 and October 14, at least seven Atlantic salmon were killed by poachers. On October 20, an additional 12 Atlantic salmon were tagged, transported and released in the same manner (Figure 3).

A further 10 Atlantic salmon were tagged and transported at the beginning of December in an attempt to increase sample size for spawning behaviours. This last batch of fish were obtained from the OMNR Fish Research Facility and Hatchery in Normandale, Ontario and were less mature, about 35% smaller and one year younger than the first batches of fish from Codrington. These fish were not observed to spawn and, because the surface of the creek froze, were not clearly visible for observations nor were they tracked successfully through the ice with the telemetry equipment. For these reasons, this last batch of released Atlantic salmon will not be considered further.

The first release group of Atlantic salmon was transported in a 400 gallon recirculating tank mounted on a trailer and oxygen and temperature in the tank was

monitored from inside the truck. The second and third release groups were transported in a 450 L bonar tub, borrowed from OMNR. An air tank was attached to the tub and delivered oxygen to the fish via an airstone. Water temperature and dissolved oxygen levels during all transports were 8°C +/- 2°C and 9.5 mg/l +/- 2 mg/l, respectively.

Chinook salmon used in this study were mature feral adults, 3-10 kg in size returning to spawn in Bronte Creek. The fish were not aged, but Chinook salmon of these sizes would normally be between the ages of two and three (Schaner *et al.* 1999). Low water levels prevented the Chinook salmon from migrating upstream to the spawning grounds of Bronte Creek. Chinook salmon remained at the mouth of the creek, in Lake Ontario and only migrated as far upstream as Highway #5 (see Figure 1), about 15 km upstream of the mouth. By the end of October, it was apparent that the Chinook would not complete their migration to the spawning grounds, so between October 23 and October 27, twenty fish were caught at the mouth by angling with barbless hooks, tagged with EMG transmitters and spaghetti tags, transported to Lowville Park and released into a recovery net-pen on the spawning grounds (Figure 2). After 48 hours of recovery, the Chinook were released one at a time into the creek. Unfortunately, female Chinook salmon did not survive longer than one day post-tagging in Bronte Creek and in fact released most of their eggs during transport from the mouth to the spawning grounds. Therefore, telemetry studies and visual observations were limited to six tagged male Chinook salmon and 10 jack Chinook.

Chinook salmon were transported in the same 450 L bonar tub and air tank as used for the second and third Atlantic salmon transports.

EMG tags were surgically implanted under the belly skin (Healey *et al.* 2003). Prior to surgery all fish were measured for length, and sex was estimated (and later confirmed after death). Weights of the fish (Table 1) were determined using a relationship between length and

weight for each species obtained from OMNR (Jim Bowlby, OMNR, *pers.comm.*, Jan. 19, 2003). The relationship for the Atlantic salmon was from the same stock of fish used in my study and the relationship for Chinook was from the feral population in the nearby Credit River.

For Atlantic salmon: $W = L^{2.0082} \times 10^{-2.1567}$

For Chinook salmon: $W = L^{2.7212} \times 10^{-4.1852}$

Fish #	sex	total length (mm)	weight (grams)	tagging date	release date	tracking time
Atlantic						
1	f	765	4308	Sept. 27	Oct. 10	34 days
2	m	640	3011	Oct. 20	Oct. 22	14 days
3	f	720	3814	Oct. 20	Oct. 22	18 days
4	f	630	2917	Oct. 20	Oct. 22	22 days
5	f	775	4422	Oct. 20	Oct. 22	13 days
6	m	640	3010	Sept. 27	Oct. 10	38 days
Chinook						
A	m	695	3535	Oct. 23	Oct. 24	12 days
B	m	925	7696	Oct. 23	Oct. 25	5 days
C	m	840	5920	Oct. 23	Oct. 24	4 days
D	m	840	5920	Oct. 31	Nov. 1	10 days
E	m	625	2648	Oct. 31	Nov. 2	5 days

Table 1: The six Atlantic salmon and five Chinook salmon tagged with EMG transmitters, observed for behaviours and interactions and energy use in Bronte Creek.

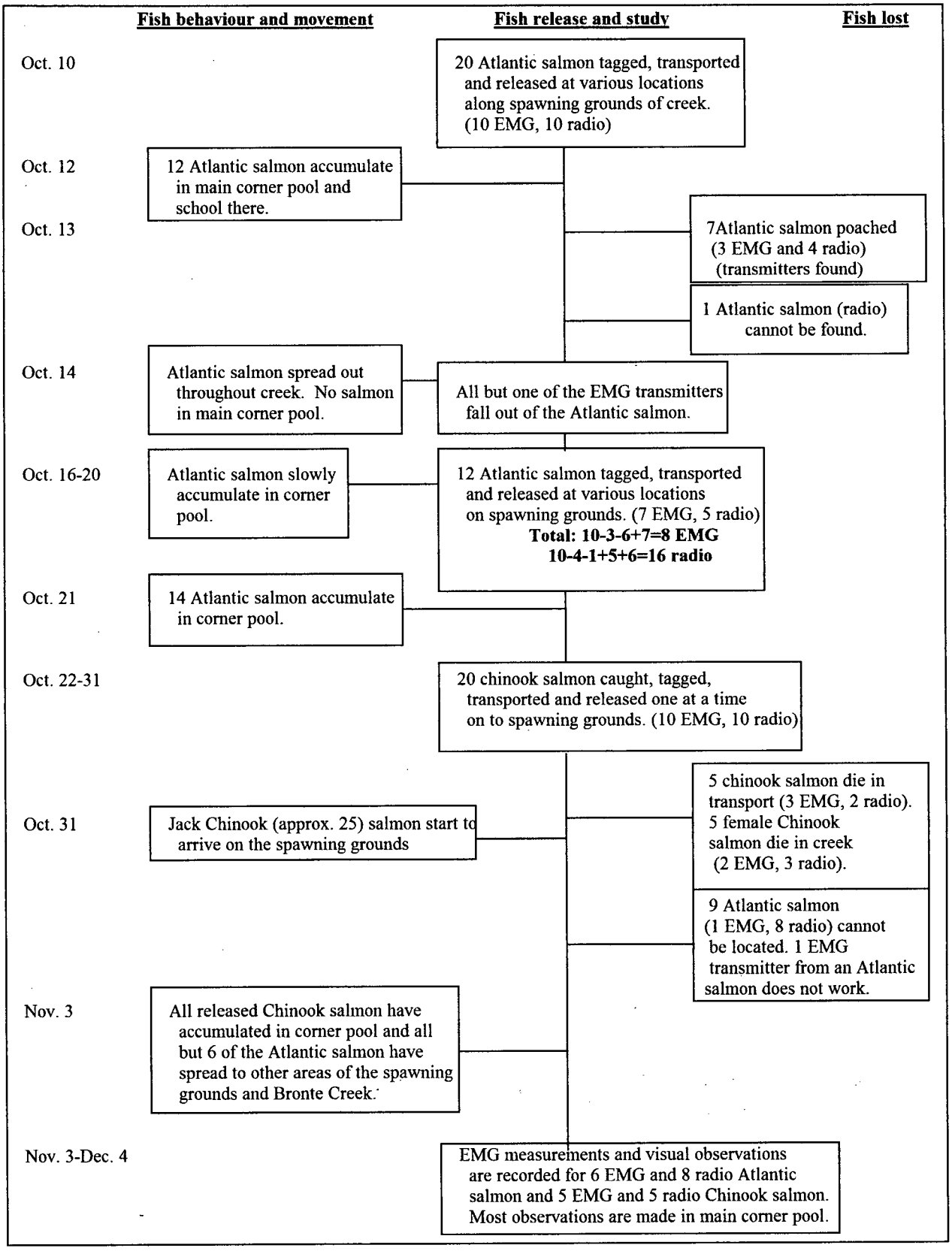

Figure 3: Time course of study showing releases of tagged fish and other significant events.

Telemetry Equipment

The telemetry equipment used in this study was identical to that used by Hinch *et al.* (1996) and was manufactured by Lotek Engineering in Newmarket, Ontario. The EMG transmitter was 5 cm long, 1.5 cm in diameter, and weighed 20 grams in air, which is less than 2% of the body weight of the fish used in this study (Kaseloo *et al.* 1992). An antenna and two teflon coated, stainless steel bipolar electrode wires (Beddow and McKinley 1998) trailed from the base of the transmitter. Each electrode wire was attached to a 14-carat solid gold tip, one cm long and one mm in diameter. When the tag was implanted these gold tips were anchored in the axial red musculature. When activated the transmitter sent pulse intervals that were proportional to electrical activity in the axial musculature. The receiver (Lotek model SRX 400) was programmed to record signals continually from an individual fish and the gain was set so that a strong signal was obtained without interference or excessive background noise. A 3-element Yagi antenna was used to track individual fish and receive EMG signals from the transmitter. The data from the receiver were downloaded daily to a laptop computer.

The transmitter is designed to detect all electrical discharges over 1-2 uV in amplitude. The signals are amplified 27,000x, rectified, and integrated, and a radio pulse is transmitted whenever the integrated signal exceeds a predetermined threshold level (150 uV) (Hinch *et al.* 1996). The integrator is then reset and the process is repeated. Therefore, the interval between the radio pulses correlates with the frequency of muscle contractions. The receiver records the time interval (in ms) between the pulses, which is negatively correlated with muscular activity.

Surgical Technique

The surgical technique used for both Atlantic and Chinook salmon is from Healey *et al.* (2003) and is similar to the technique used by Hinch *et al.* (1996) and Okland *et al.* (1997). The fish were anaesthetized in a solution of 1 part clove oil to 150 parts isopropyl alcohol at a concentration of 60 parts per million, following the procedures of Cooke *et al.* (2000).

A 2.5-3 cm saggittal incision was made through the skin on the ventral surface of the fish 15 cm posterior to the pectoral girdle. A blunt probe was used to create a 10 cm pocket in the skin extending forward from the incision. The transmitter was slipped into this pocket and the electrodes implanted in the red muscle just above the lateral line by pushing them under the skin with a hollow probe. The gold tips were placed approximately one cm apart and electrode placement was kept consistent at the posterior portion of the dorsal fin (Beddow and McKinley 1999). The incision was then sutured with six or seven sutures, using 2.0-3.0 size Ethicon sutures with silk thread and a 28 mm bent cutting needle from Tyco Healthcare. Tissue glue was added to the suture, as well as a few drops of an antibacterial agent, Betadyne. The total surgery time for each fish was less than 10 minutes. EMG tags were implanted subcutaneously to ensure that no water would enter the body cavity, which may effect the release of the eggs during spawning in females (Kaseloo *et al.* 1992; Healey *et al.* 2003).

Several fish were tagged with simple radio transmitters, implanted into the eosophagus through the mouth after the fish had been anaesthetized. All fish were allowed to recover from surgery from 48 hours to 2 weeks, depending on transport times and distances.

Atlantic salmon were also tagged for visual identification with orange Floy tags implanted with a tagging gun under the dorsal fin. Chinook salmon were tagged for visual identification with yellow spaghetti tags, which were threaded through the musculature posterior to the dorsal fin and tied across the back.

Telemetry and Visual Observations

EMG telemetry and visual observations on Atlantic salmon and Chinook salmon in Bronte Creek were carried out from October 29 until December 4, 2002. Individual fish were located by their unique tag frequency using the portable receiver and antenna. Once a fish was located I recorded its general physical condition, its location in the stream and relative to other fish, and observed its behaviour for 30 minutes. Fish were observed and EMG readings were recorded along the entire 1.5 km stretch of spawning grounds. However, most of the fish were congregated after release within 100m of the deepest and largest corner pool on the spawning grounds. The pool was 2.5 m deep, 5 m wide and 8 m long and consisted of a large area of open space, a few large rocks, and two dark caves under the creek bank. Most of the behaviours, including interactive behaviours, observed in this study were seen in or around this corner pool. Despite the crowding of the fish, the telemetry equipment allowed the individual fish to be pinpointed exactly and thus observations could be assigned to a specific individual. Fish were fully visible in the pool at most times of the day however, the water became dark and murky after storms so that the fish could not be observed at these times. No recordings were made after the sun went down, as the fish in the pool could not be seen for behavioural observations. However, EMG signals that were obtained at various times throughout some evenings were consistent with those obtained throughout the day. Healey *et al.* (2003) found that there was no significant difference between EMG signals and subsequent energy consumption during the day and the night in sockeye salmon.

EMG readings were continually recorded and archived in the receiver for an individual fish and at the same time a tape recorder was used to record the time of day, EMG reading and

the associated behaviour. These tape recordings were later used to identify EMG readings for specific behaviours and frequencies of these behaviours. Periodically, fish were observed specifically to determine the duration of specific behaviours. A stop watch was used to time the duration of each behaviour as it occurred.

The behaviours observed in this study were similar to those observed in other studies, although no spawning behaviours were observed because the fish did not spawn. The behaviours recorded were:

1) Resting/Hiding: the fish is not moving and is sitting on the bottom of the creek or on rocks or hiding in a cave.

2) Holding: the fish is swimming constantly in one spot without forward progress.

3) Casual Swimming: the fish is swimming forward at a casual to cruising speed.

4) Holding @ other species: a male Chinook salmon and a female Atlantic salmon hold beside one another and male Chinook salmon performs "rubbing" behaviours (see results section for a more detailed description).

5) Burst Swimming: the fish sprints or darts forward.

6) Charging: one fish charges at another fish with it's mouth open.

7) Bunting: one fish charges at another fish, but the mouth is closed. The fish pushes the other fish.

8) Receiving a charge (or bunt): the fish exhibits a "flight" response and bursts away from the charger.

9) Chasing: one fish swims after another fish.

Permits and Animal Care

A license to stock fish (license # 1002636) was obtained from the Ontario Ministry of Natural Recourses. A license to collect fish for scientific purposes (license # 1002767) was also obtained from the ministry in order to transport Chinook salmon from the mouth to the spawning grounds in Bronte Creek. Both of these licenses were issued under Part I of the Fish Licensing Regulation made under the Fish and Wildlife Conservation Act of 1997. As well, all animals used in this study were treated with care as outlined in the OMNR Fisheries and UBC Animal Care Class Protocol (#A01-0003).

2.2 Laboratory Work

Relationships between EMG signal, swimming speed and oxygen consumption for Atlantic salmon were determined with captive fish in a swim tunnel respirometer. The swim tunnel was assembled and used in the wet-lab in the Forest Science building at the University of British Columbia (UBC). The lab also contained three round fibre-glass tanks of 4000 L each with a flow through system of Vancouver city well water, which was dechlorinated using sodium thiosulphate prior to entering the fish tanks. These tanks held Atlantic salmon prior to surgery, post-surgery, and prior to swim tunnel trials. Because of a lack of a saltwater source at UBC, two groups of fish were first acclimated at the West Vancouver Department of Fisheries Research Station (West Van lab) and then transported for swim tunnel trials to the UBC lab. The final group of fish was acclimated at the UBC lab.

Fish, Transport and Acclimation

The Atlantic salmon used in the swim tunnel were maturing adults, 2-3 years old, and 1.5 to 3 kg in size. The fish were obtained from Agrimarine Industries on Vancouver Island in B.C. The fish were seined at the farm, retrieved by dip-netting and transported to the West Van lab (groups 1 and 2) or directly to UBC (group 3). At the West Van lab the fish were not fed and were held in covered, round, fibre-glass, 4000 L tanks, outdoors with a flow through system and were acclimated to freshwater by gradually increasing the freshwater flow and decreasing the seawater flow into the tanks over a two-week period. After acclimation, the fish were transported to the Forest Science building at UBC for surgery, recovery and swim tunnel trials. The third group of fish was transported directly from the tank farm to the UBC lab and was acclimated to freshwater, over a 24-hour time period in a covered tank. This change in procedure was made because of high mortality in the first two groups of fish.

All transports of fish were made in an insulated 500 L steel chamber, aerated via an air compressor. During all transports, acclimation periods, and holding times, the water temperature was kept between 9 and 14°C and the dissolved oxygen between 7.5 and 10 mg/l. From the three groups of fish, swim tunnel measurements were completed on ten healthy fish (Table 2).

Fish #	sex	total length (mm)	weight (grams)	tagging date	swim date
1	M	510	870	May 9	May 10
2	M	590	2200	May 10	May 11
3	M	578	2100	May 11	May 12
4	F	561	2025	May 17	May 18
5	M	613	2120	May 19	May 20
6	M	590	1150	July 1	July 2
7	F	632	2210	July 2	July 3
8	F	572	1190	July 4	July 5
9	F	640	1770	July 5	July 6
10	M	605	1510	July 6	July 7

Table 2: Characteristics of the 10 Atlantic salmon used in the laboratory study in the respirometer.

The stress of transporting fish must be taken into account for the Chinook salmon and the Atlantic salmon in Bronte Creek, as well as for the Atlantic salmon in the respirometer swim trials. Transporting is one of the highest stressors to fish and a suggestion to help alleviate this stress after transport is a lengthy recovery time (Sandodden *et al.* 2001). Recovery time for the fish in this study, post-transport, ranged from several days to two weeks. This recovery time is well above the recommended 48 hours (Sandodden *et al.* 2001) and so it is expected that stress of transport had little effect on the results of this study.

Surgical Technique

The surgical technique used on the Atlantic salmon in the respirometer studies was similar to that performed on the fish in Bronte Creek. The fish in the UBC lab were anaesthetized using tricaine methanosulphonate (MS222) and then measured for length, depth, width, weight, and the sex was estimated and later confirmed after death. The EMG transmitters, including the electrode wires and gold tips, were implanted in the same manner as the surgery on the fish in Bronte Creek, except that the transmitters were placed into the body

cavity rather than under the skin. The ventral incision was made longitudinally and extended into the body cavity. The transmitter was then placed into the cavity among the pyloric caeca of the fish. Instead of trailing through the sutures, the antenna was directed through a hole in the body wall posterior to the incision. Tag implantation in the body cavity is fully described by Hinch *et al.* (1996). Following surgery, the fish was held in the swim tunnel for approximately 15 hours before the initiation of swim trials.

Respirometer

The swim tunnel used in this study was a mobile Brett-type tunnel with a tunnel diameter of 26 cm and a volume of 417 L. Dechlorinated Vancouver city water was gravity fed from a reservoir in the lab into the tunnel at a temperature between 11 and 14°C. The swim chamber was transparent, which allowed for video recording both the fish and associated EMG readings from the Lotek receiver, which was displayed on a monitor in a picture-within-picture format. These video tapes were later used to count tailbeats, measure tailbeat amplitude, and record associated EMG readings. The swim tunnel was also equipped with an electrical device in the back of the swimming tube which gave off a 5V shock whenever the caudal fin of the fish would touch the grid. This electrical charge encouraged the fish to swim near the centre of the swim tube.

Oxygen consumption during swim tunnel trials was measured using an Oxy probe which was inserted into an airtight portal in the tunnel. The probe was connected to a receiver and a laptop computer where the incoming oxygen measurements were recorded.

The swim tunnel was cleaned prior to use, at completion of the swim trials and a few times throughout with an anti-bacterial agent, Wescadyne.

Swim Trials

Swim trials for the Atlantic salmon were carried out during the spring of 2003. After surgery, an individual fish was allowed to recover and habituate to the tunnel over night at a water velocity of 0.4 BL/s. The fish did not swim at this speed and in fact simply sat at the rear of the tunnel. The next morning a test swim was performed to identify an approximate maximum swimming speed for the fish. The water velocity in the tunnel was increased 0.25 BL/s every five minutes until the fish fatigued. Fatigue was measured by the fish's inability to move off of the shocking grid at the back of the tunnel within 20 seconds. After the test swim, the fish was allowed to recover for two hours at 0.4 BL/s before the actual measure of swimming performance. For the actual swim trial the water velocity was increased 0.15 BL/s every 15 minutes up to half of the maximum swimming speed and then every 30 minutes after (Jain *et al.* 1997). During the last 10 minutes of every swim trial step oxygen measurements were recorded from the tunnel. The affluent water was turned off throughout the oxygen recordings and turned on again at completion of the recordings to flush the tunnel with fresh and oxygenated water. EMG pulse intervals were only recorded when the fish was swimming in a consistent manner in the middle of the tunnel.

A blocking effect of the fish was taken into account when estimating actual swim speed in the swim trial (Bell and Terhune 1970):

Corrected Swim speed = Velocity of the tunnel (cm/s) x (1 + Es)

where $Es = 0.8 \times (1/2 \times \text{fork length/thickness}) \times (\text{XS area of fish/XS area of tunnel})^{3/2}$

where thickness = (depth + width) / 2

XS area of fish = π x depth/2 x width/2

XS area of tunnel = πr^2

Tailbeat frequency was determined from the videotapes by counting the number of tailbeats for a period when the fish was swimming in a consistent manner and EMG was being simultaneously recorded. Tailbeats per second was determined by dividing the counted tailbeats by the period of measurement. Values for tailbeat frequency and associated EMG were determined for each velocity step in a swim trial. As well, a ruler was taped to the monitor and tailbeat amplitude was recorded by measuring the distance the caudal fin moved during one complete tailbeat.

Permits and Animal Care

A license to import/transfer live fish within British Columbia (license # 9747) was obtained from the Department of Fisheries and Oceans pursuant to section 56 (1) of the Fishery (General) Regulations made under the Fisheries Act. As well, all animals used in this study were handled with care as outlined in the UBC Animal Care Class Protocol (# A01-0003).

2.3 Statistical Analysis

The critical swimming speed (Ucrit) of the Atlantic salmon in the swim trials was calculated as in Brett (1965):

$$Ucrit = Uf + (tf / ti \times Ui)$$

where Uf is the water velocity of the last fully completed increment; tf is the time spent on the last water velocity increment; ti is the time period for each completed water velocity increment (30 minutes); and Ui is the water velocity increment (0.15 BL/s).

The computer program output for oxygen consumption was given in millivolts and so was converted to mg/l by multiplying the slope of the linear relationship between millivolts and mg/l, which was calibrated in the swim tunnel prior to swim trials. Oxygen consumption and time relationships (mgO_2/s) were then determined for each fish at each swimming speed. The slopes of these relationships were used in the following formula to estimate oxygen consumption in $mgO_2/kg/hr$ (Grottum and Sigholt 1998; Geist *et al.* 2000):

$mgO_2/kg/hr$=3600x slope(mg/s)x(volume of tunnel(L)-mass of fish(L))/mass of fish(kg)

where the mass of the fish in litres is estimated based on: 1 kg = 1 L (Geist *et al.* 2000).

3.0 Results

3.1 Field Study

The air temperature in Lowville Park during the time of the field study ranged from 35°C in the summer to –25°C in the early winter. Water temperatures in Bronte Creek ranged from 18°C in the summer to 3°C under the ice in the early winter. Dissolved oxygen levels in the creek ranged from 8.5 to 12.5 mg/l, decreasing after a rainstorm when the water became silty. The water velocity in the main corner pool of the spawning grounds was 0.19 to 0.25 m/s and increased to a maximum velocity of 0.78 m/s after rainstorms. Due to limited rainfall and resultant low water levels in the fall the water velocity of the creek remained low. Water level, measured at the pool where most fish congregated, increased only 7 cm between July 1 and Dec. 2. Water samples taken on Aug. 28 and Nov. 6 were of similar quality (phosphate 0.05 mg/l and 0.04 mg/l; nitrate 1.29 mg/l and 1.60 mg/l; alkalinity 168 mg/l and 215 mg/l; total dissolved solids 602 mg/l and 440 mg/l; pH 8.10 and 8.21; and *E. coli* counts 110 cfu/100ml and 57 cfu/100ml, respectively).

Four female and two male Atlantic salmon and five male chinook salmon, with EMG tags, were observed for behaviours and movements in Bronte Creek on the spawning grounds in Lowville Park. In addition, 8 Atlantic salmon and 5 jack Chinook with radio tags were observed for behaviour frequency and duration. Figure 3 summarizes the following narrative.

Thirty-two Atlantic salmon were released onto the spawning grounds in Lowville Park prior to the arrival of any Chinook salmon. At release the fish were distributed individually and in pairs at various locations along a one km stretch of the spawning grounds. Immediately upon release, the fish burst away and hid under rocks, log jams, or under the creek bank. The Atlantic salmon were only rarely observed to explore the creek and all but one of the

fish, which was found at the upstream dam barrier of the spawning grounds, remained within 800 m upstream of the corner pool (before the Chinook salmon were released). Most frequently, when an Atlantic salmon was located, it was found resting among rocks near the edge of the creek. Atlantic salmon were also seen resting among logs and resting or holding under creek banks. Atlantic salmon were frequently found resting or holding under the canopies that leaves created on rocks and logs during the autumn.

Within one day following release, 12 of the Atlantic salmon had moved into the main corner pool of the spawning grounds and held in this pool in a schooling fashion. The remaining Atlantic salmon remained hidden under rocks, cut banks, and log jams along the creek, upstream of the corner pool. The group of fish in the corner pool were observed to hold continuously as a school and EMG recordings were obtained for this behaviour. No interactions were observed within the species. However, four large carp were also seen in this corner pool in the early summer and remained in the pool throughout the time of the study. The carp remained most of the time at the back of a deep cave near the bottom of the pool but two or three times a day they would come up from the bottom, casually swim around the pool in the middle of the water column and then return to the cave at the bottom of the pool. When the carp performed this action, the Atlantic salmon would scatter to the edges of the pool. Within 10 minutes of the carp's exit, the Atlantic salmon would return to the centre of the pool and hold together again in a school-like fashion. Several Atlantic salmon could be identified by external characteristics and they were observed to occupy consistent positions within the school, returning to these positions after being disturbed by the carp. The hierarchy within the school continued until the arrival of the Chinook salmon.

The carp appeared to patrol the pool less frequently after the Chinook arrived. When the carp made an appearance the Chinook salmon did not change their behaviours or positions in the

pool. Atlantic salmon continued to scatter when the carp appeared, leaving only the Chinook salmon and the carp in the pool, but would reappear in the pool within 5-10 minutes following the exit of the carp. A Chinook salmon would occasionally approach a carp and the carp would burst away.

Fifteen Chinook salmon were released one at a time from a recovery pen 150 m downstream of the main corner pool. Immediately following release, the Chinook salmon burst downstream of the release site and moved to the edges of the creek. The Chinook salmon were observed to explore the creek along a 1 km stretch downstream of the corner pool, however within two days of the release, all of the Chinook salmon had grouped together in the main corner pool and all but six of the Atlantic salmon had disappeared from the pool. Some Atlantic salmon were seen in the caves of the pool, in a log jam upstream of the pool, and some Atlantic salmon were found one km upstream of the pool by the dam, at the upstream limits of the spawning grounds. Some radio and EMG signals from Atlantic salmon completely disappeared from the spawning grounds and transmitters were later found about 30 km downstream near the mouth of the creek. The Atlantic salmon that remained in the corner pool, once the Chinook were released, were later identified as being all mature females and only several weeks away from egg release (carcasses were found at various locations in the creek from mid-November to early December).

Most of the observations of behaviour and interactions within and between species were seen in the corner pool. Additional observations were made near the park's pumphouse, about 150 m upstream of the corner pool, and at a large maple tree, about 500 m upstream of the corner pool (Figure 2). Observations at these locations included interactions between a large, EMG-tagged male Chinook salmon and several jack Chinook salmon, interactions between these fish and one radio-tagged male Atlantic salmon hiding in the rocks at the edge of the creek, and

interactions within a large group of jack Chinook salmon. Most of these jacks arrived on the spawning grounds around Oct. 31 (Figure 3) and had extensive physical wounds from their migration upstream. The jacks were observed to travel in groups or pairs and explored the spawning grounds to a great extent. Most of the jacks swam the length of the spawning grounds within the month of November, stopping often to hold beside large Chinook salmon or to hold at the edges of the creek or in log jams. An Atlantic salmon was seen to charge at a jack Chinook twice, but most of the time the jacks would charge the Atlantic salmon when they came into contact along the creek, or simply hold beside the Atlantic for an hour or two and them move on. Jack Chinook salmon were also observed to interact in the main corner pool, being charged at by larger Chinook salmon and occasionally charging an Atlantic salmon in the pool.

The average duration (Figure 4) of a burst swimming behaviour for Chinook salmon was 1.64 s (SE=0.13) and the average frequency (Figure 5) of the behaviour was 1.54/hr (SE=0.01). Charging occurred an average of 4.33/hr (SE=0.01) and lasted 0.74 s (SE=0.04). Bunting occurred an average of 1.38/hr (SE=0.03) and lasted 1.13 s (SE=0.11). Larger Chinook salmon charged Atlantic salmon and jack Chinook, and jack Chinook charged one another. The behaviour of bursting away after receiving a charge occurred an average of 0.48/hr (SE=0.01) and occurred primarily because jack Chinook were charged at by larger fish of both species throughout the field study. Large Chinook were never charged by jack Chinook or Atlantic salmon. The average duration of the burst after receiving a charge was 1.32 s (SE=0.16). Chinook salmon chased other Chinook salmon an average of 0.8/hr (SE=0.03) and only very rarely were seen to chase Atlantic salmon. Chasing lasted an average of 2.68 s (SE=0.38). Chinook salmon were seen to rest on the bottom an average of 13.69% (SE=0.05) of the time, performed casual swimming 12.43% (SE=0.03) of the time, performed a holding behaviour

67.09% (SE=0.06) of the time, and hid under rocks 3.82% of the time (SE=0.02). This time budget was based primarily on observations made in the main corner pool of the spawning grounds.

Throughout the study, most of the Atlantic salmon that were in the main corner pool and all of the Atlantic salmon in other areas of the creek remained hidden under rocks and in caves or could not be found. Thus, the duration and frequency of behaviours (Figure 4 and 5, respectively) were determined from the Atlantic salmon that could be seen in the water column most of the time. These Atlantic salmon performed a burst swimming behaviour an average of 0.53/hr (SE=0.01) for females and 0.33/hr (SE=0.03) for males and the burst lasted an average of 1.98 s (SE=0.26) for both sexes. Female and male Atlantic salmon were charged by larger Chinook an average of 2.20/hr (SE=0.04) and 2.00/hr (SE=0.02), respectively. A few Atlantic salmon were seen to charge one another an average of 2.80/hr (SE=0.02) and chase 1.77/hr (SE=0.01). These relatively high rates of chasing and charging are due to the fact that 2 Atlantic salmon exchanged charges and chases for an entire day. The other Atlantic salmon were seldom observed charging or chasing. The average duration of a charge was 1.07s (SE=0.07). Receiving a charge lasted an average of 1.44 s (SE=0.15) and chases lasted 3.12 s (SE=0.43). Female and male Atlantic salmon were seen to rest on the bottom an average of 36.32% of the time (SE=0.21) and 1.19% of the time (SE=0.01), to perform casual swimming 5.39% of the time (SE=0.03) and 7.53% of the time (SE=0.02), and to perform holding behaviour for 39.80% of the time (SE=0.21) and 90.75% of the time (SE=0.02), respectively. Female Atlantic salmon were seen hiding under rocks an average of 15.9% of the time (SE=0.09) and male Atlantic salmon were never seen performing this behaviour.

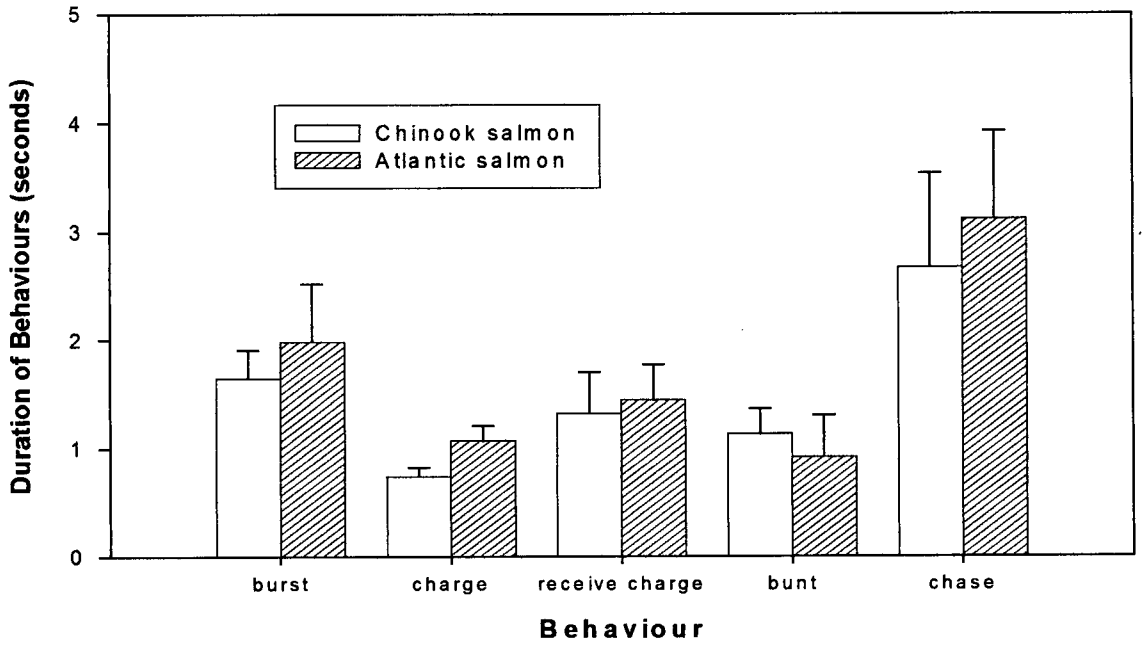

Figure 4: The average durations of behaviours of Chinook salmon and Atlantic salmon in Bronte Creek. The error-bars represent 95% confidence intervals for the mean duration of each behaviour.

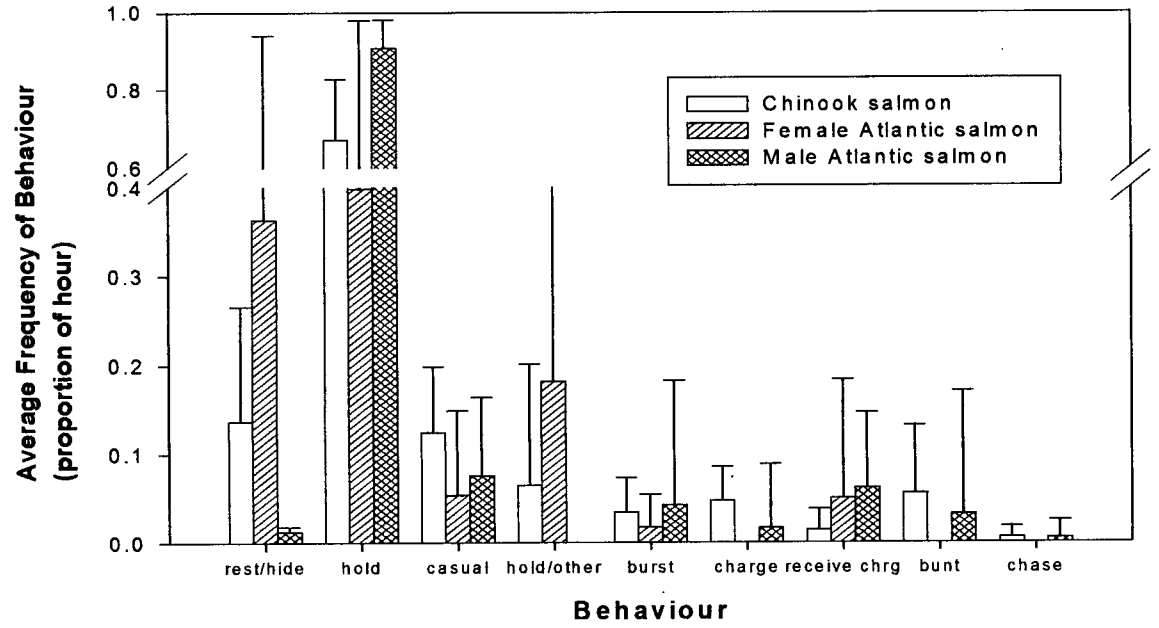

Figure 5: The average proportion of an hour spent performing behaviours by Chinook salmon and Atlantic salmon in Bronte Creek. Error-bars represent a 95% confidence interval for the mean percent time of the behaviour. (n=4 female Atlantic salmon, 2 male Atlantic salmon, 5 male Chinook salmon)

Although no spawning was observed during the study, possible interspecific mating behaviour was observed. Two female Atlantic salmon that remained in the corner pool after the Chinook salmon had arrived, spent most of their time holding independently (in a single position) in the middle of the water column near the centre of the pool. Two large Chinook salmon performed holding and defensive behaviours around each of these Atlantic salmon females throughout the time the fish were on the spawning grounds. Both of the Chinook salmon and both of the Atlantic salmon were tagged with EMG transmitters. Each of the Chinook salmon held beside each of the Atlantic salmon, chased away any other Chinook or Atlantic salmon that came near, and would sometimes rub up against the Atlantic salmon. The female Atlantic salmon did not change their positions or behaviour at any time.

The last Chinook carcass was found on November 22. Out of the originally released 32 Atlantic salmon, 7 fish were poached and 14 carcasses were found between Nov. 9 and Dec. 1 along Bronte Creek from the main corner pool to approximately 10 km downstream. It is unclear what happened to the remaining 11 Atlantic salmon. Some transmitters were found near the mouth of the creek, so it is assumed that some of the Atlantic salmon swam downstream to Lake Ontario.

Some EMG values were excluded for the fish in Bronte Creek and these included readings from individual fish that were only observed from time to time. The EMG values that were used in this study are from fish that were observed for most of the days of the study in Bronte Creek.

EMG values that had extensive chevron symbols following the readings on the receiver were also excluded as later it was realized that these symbols were seen when the transmitter had fallen out of the fish. This problem was not reported in other studies (Healey *et al.* 2003). After

the transmitter had been surgically implanted subcutaneously and while the fish were recovering, some of the tagged salmon would rub their bellies against the bottom of the tank or the bottom of the creek. The transmitters would then fall out "head first" through the skin, with the suture still in place, and the electrodes would be ripped out when the transmitter snagged on a rock, etc. The excellent tracking capabilities of the Lotek telemetry equipment allowed for the retrieval of transmitters that fish lost in the creek. There did not appear to be any other obvious effect of the transmitters on the fish and, although reduced buoyancy of tagged fish has been recorded (Perry *et al.* 2001), no obvious effects of appropriate sized transmitters on fish have been found (Adams *et al.* 1998; Beddow and McKinley 1992; Kaseloo *et al.* 1992; Thorstad *et al.* 2000).

3.2 Swim Tunnel Results

The Atlantic salmon did not show obvious signs of stress from either transport or transfer to freshwater. In their holding tank they rested on the bottom or sometimes swam with the current as individuals or as a group. Fish in the respirometer rested on the bottom of the tunnel at very low water velocity and only started to swim between 0.6 and 0.75 Body Lengths (BL)/s, swam back and forth throughout the tunnel at higher speeds, and displayed erratic swimming and more vertical movement at their highest swimming speed, just prior to failure. Most of the Atlantic salmon spent much of their time at the back of the tunnel during most steps in the swim trials and two fish remained close to the grid at the front of the tunnel for all steps of the swim trials.

A critical swimming speed (Ucrit) was determined for each fish in the swim tunnel (Figure 6). The average critical swimming speed for the Atlantic salmon was 1.25 BL/s (73.28 cm/s). Fish #1 had the highest Ucrit at 1.67 BL/s (85.23 cm/s) and fish #8 had the lowest Ucrit at 0.63 BL/s (35.76 cm/s).

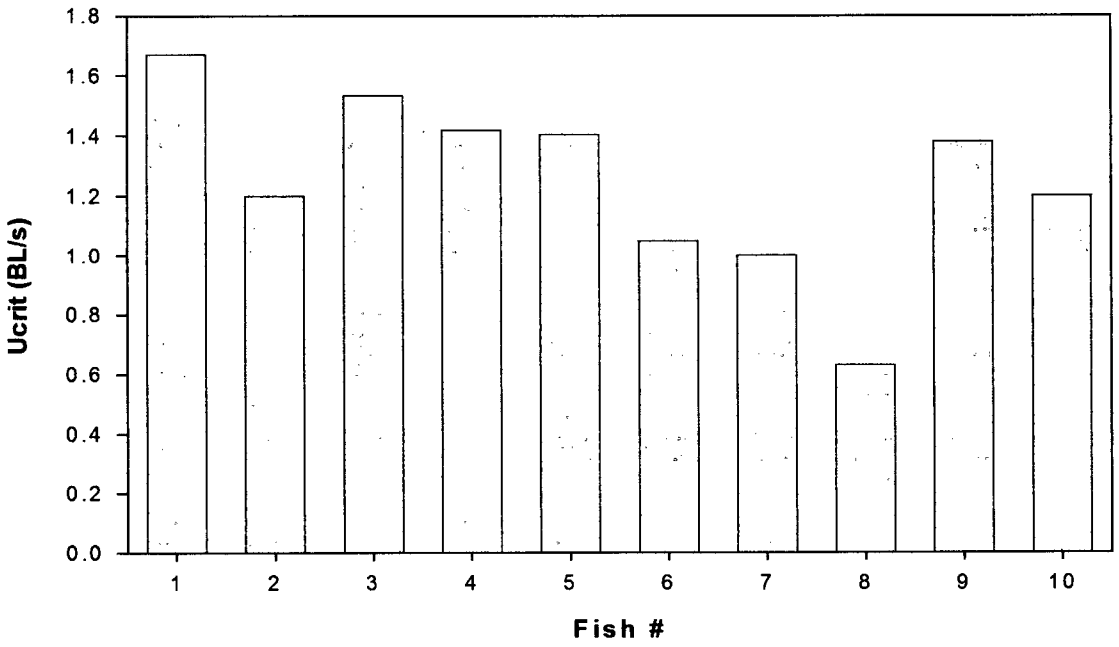

Figure 6: The critical swimming speed for 10 Atlantic salmon in the respirometer.

Oxygen consumption was determined for only the last 6 of the fish shown in Figure 6, due to mechanical and technological problems with the oxygen probe at the start of the swim trials. Figure 7 shows the oxygen consumption of Fish #10 at different stages in the swim trial. Note that oxygen concentration did not recover to full saturation after each measurement. Care was taken to ensure that oxygen concentration in the tunnel never dropped below 7 mg/l. Oxygen consumption in $mgO_2/kg/h$ was calculated for each swimming velocity and plotted in relation to swim speed (Figure 8).

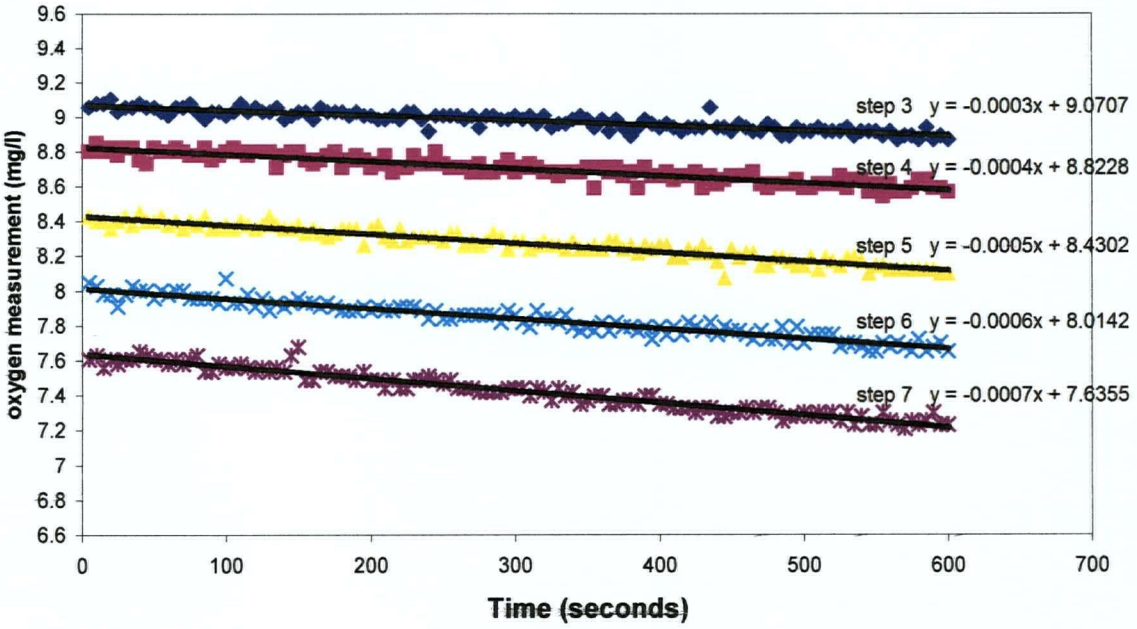

Figure 7: The oxygen consumption of Fish #10 for swimming step 3 to 7. The linear equation for each step is displayed and the slopes of these lines were used to determine oxygen consumption in mg/kg/hr for the fish at each swimming speed.

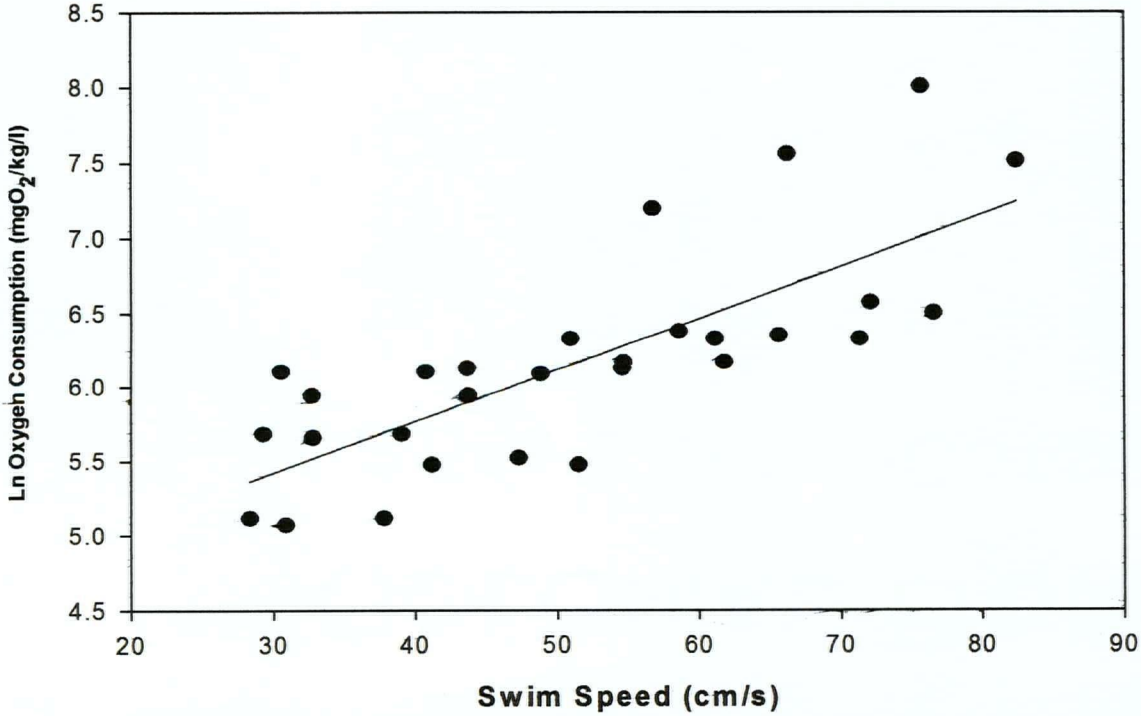

Figure 8: The oxygen consumption in relation to swimming speed for Atlantic salmon during swim trials in the respirometer. The line is the regression of lnO2 on swim speed. $r^2 = 0.5927$, n=6

3.3 Energy Expenditure

Initially, I planned to estimate energy expenditure for Atlantic salmon by estimating tailbeat frequency (TBF) from the relationship between TBF and EMG and then to convert this to swim speed and energy cost, as in Healey *et al.* (2003) and Hinch and Rand (1998). Hinch and Rand (1998) found a linear relationship between TBF and EMG pulse for sockeye salmon (*Oncorhychus nerka*) and used this relationship together with relationships between TBF and swim speed and the size of the fish to determine energy use (see formulae in Healey *et al.* (2003)). Figure 9 shows the TBF and EMG relationship for Atlantic salmon from the swim tunnel measurements. The data are extremely scattered and do not define a clear relationship between TBF and EMG. It was apparent when reviewing the videotapes that tailbeat amplitude varied with swim speed as well as TBF. Therefore, tailbeat amplitude (TBA) was also calculated for several fish and the product TBA x TBF compared with EMG (see Figure 10 and 11 for Fish #7). The relationships of TBF to EMG and TBF x TBA to EMG both showed high variance but including TBA in the relationship improved the relationship (the variance explained increased from 5 to 38%). Webb (1971) found that amplitude varied so much between 2 and 5 tailbeats/s that TBF alone was not a reliable indicator of swim speed. Because of this fact, energy expenditure for Atlantic salmon was determined using relationships with swim speed as in Cooke *et al.* (2000), Beddow and McKinley (1998), Okland *et al.* (1997), and Kaseloo *et al.* (1992) and TBF was eliminated from the statistical analysis.

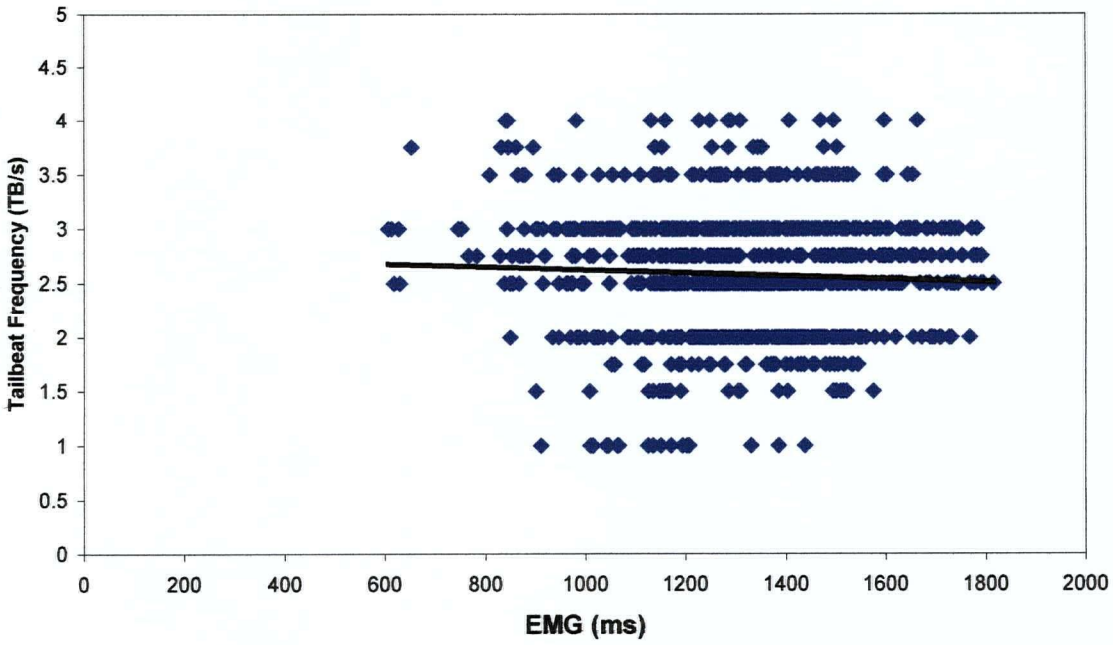

Figure 9: Relationship between the tailbeat frequency of Atlantic salmon during swim trials and associated EMG pulse intervals. $r^2 = 0.0025$, n=10

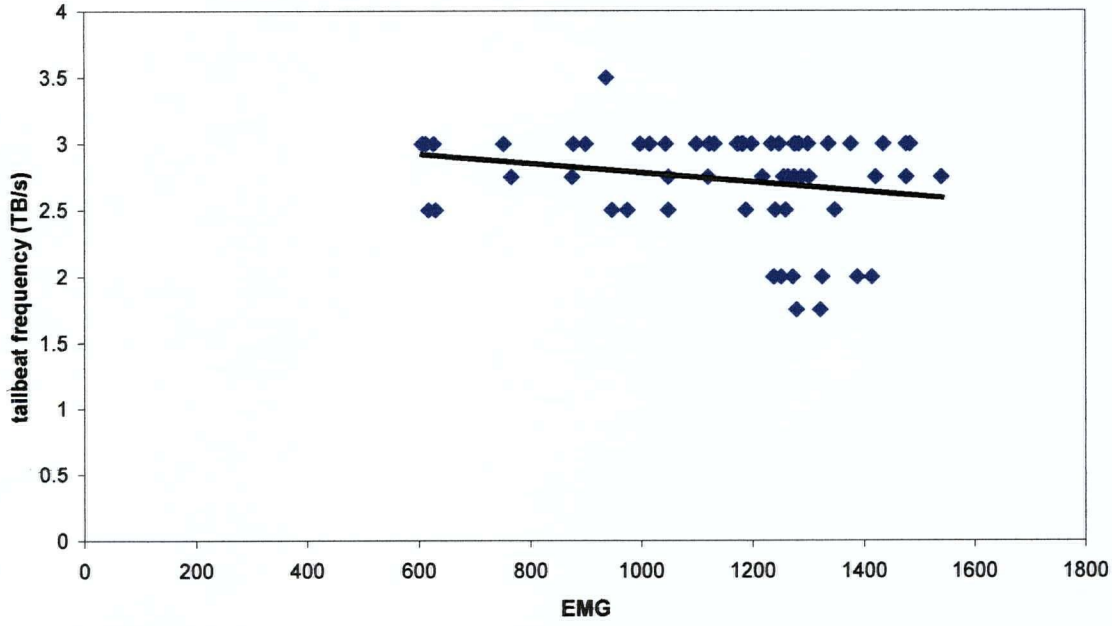

Figure 10: Relationship between the tailbeat frequency of Atlantic salmon #7 during swim trials and associated EMG pulse intervals. $r^2 = 0.0506$, slope = -0.0004.

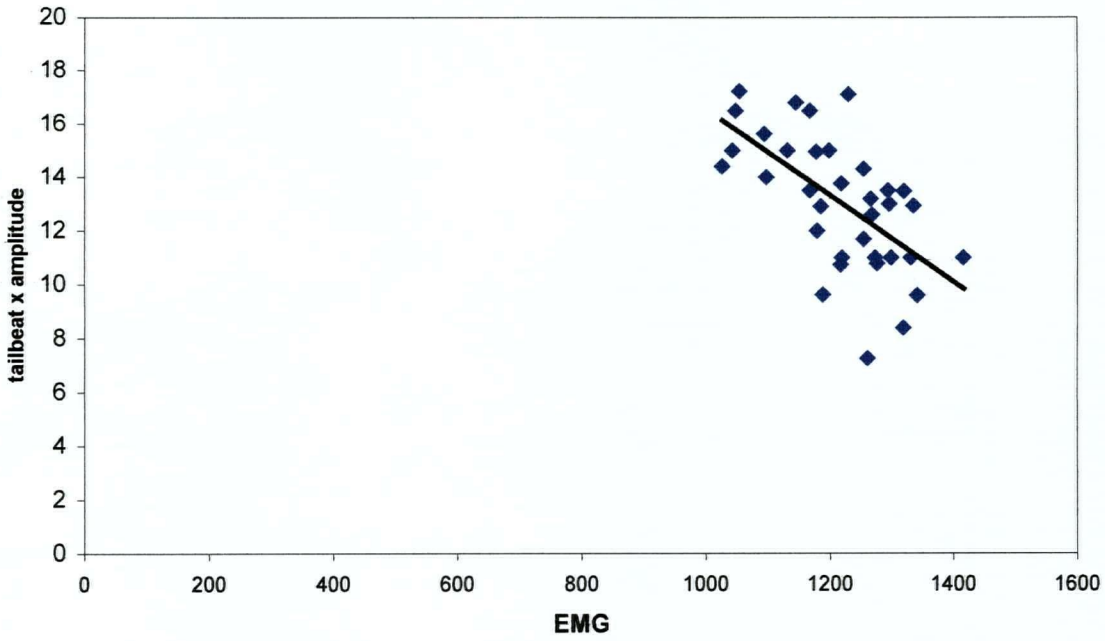

Figure 11: Relationship between the product of tailbeat frequency and tailbeat amplitude for Atlantic salmon #7 during swim trials and associated EMG pulse intervals. $r^2 = 0.3797$, slope = -0.0161

The relationship between EMG (ms, averaged for each fish for each swim step) and swim speed (cm/s) in the swim tunnel was linear (Figure 12).

$$y = -5.0293x + 1611.1$$

where y is EMG (ms) and x is swim speed (cm/s). This model was used to find swim speed numbers for the fish in Bronte Creek using the EMG values obtained in the field study.

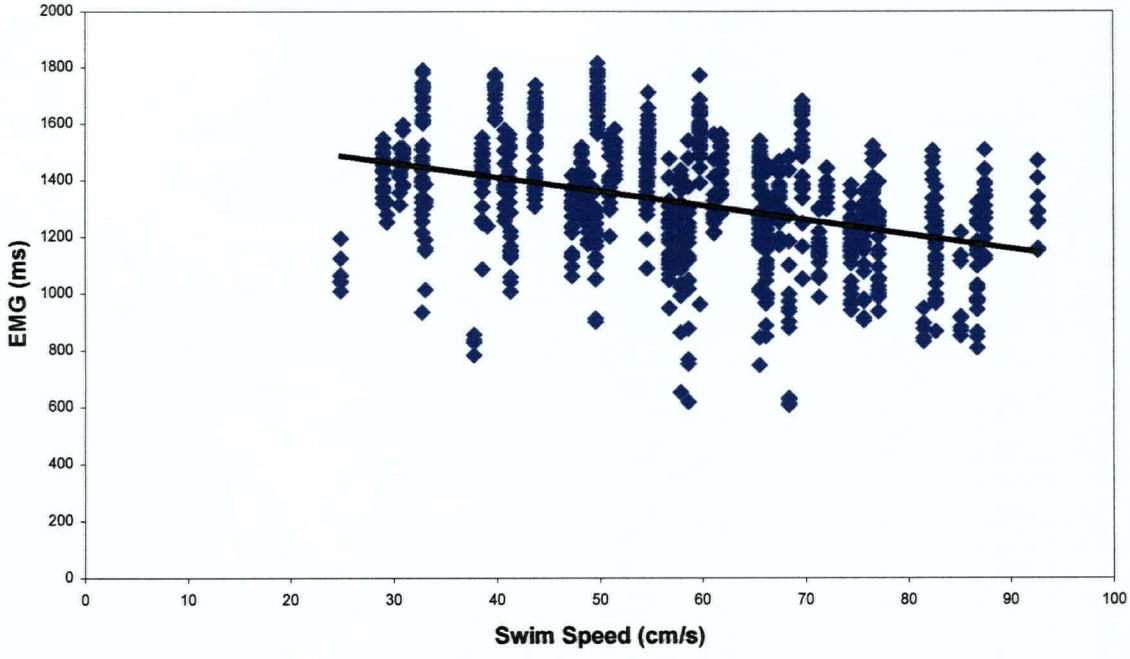

Figure 12: Relationship between the average EMG pulse intervals and swim speed for 10 Atlantic salmon during swim trials. $r^2 = 0.1476$

Once swim speed values were identified for the Bronte Creek fish, oxygen consumption was calculated for each Atlantic salmon based on the exponential relationship in Figure 8.

$$\text{Ln}(y) = 0.0348x + 4.3789$$

where y is oxygen consumption (mgO2/kg/h) and x is swim speed (cm/s).

Oxygen consumption was also determined for Chinook salmon using a relationship between oxygen consumption (mgO2/kg/h) and EMG pulse rate (pulses per minute) for adult Chinook salmon from Geist *et al.* (2000).

$$y = 0.07x + 2.18$$

where y is the natural log of oxygen consumption (mgO2/kg/h) and x is the EMG pulse rate in pulses per minute.

Values for oxygen consumption were transformed into energy measurements by multiplying by the oxycalloric coefficient, 3.25 cal/mgO_2, from Brett (1995). Figure 13 shows the average energetic cost of each behaviour for the Chinook salmon and for the male and female Atlantic salmon in Bronte Creek. The energy values were then multiplied by the duration of individual behaviours to determine the energetic cost of the behaviour (Healey *et al.* 2003).

Cb = E x (duration of behaviour in seconds/3600)

where Cb is the cost of the behaviour (cal/kg/h) and E (cal/kg/h) is the calculated energy from the previous step. Each of these values was then multiplied by the frequency of the behaviour in one hour and then by 24 to obtain the E/Day. The resulting values were then averaged for each individual fish and then averaged for each species to determine the average daily energy cost of a behaviour for each species and each sex (Figure 14).

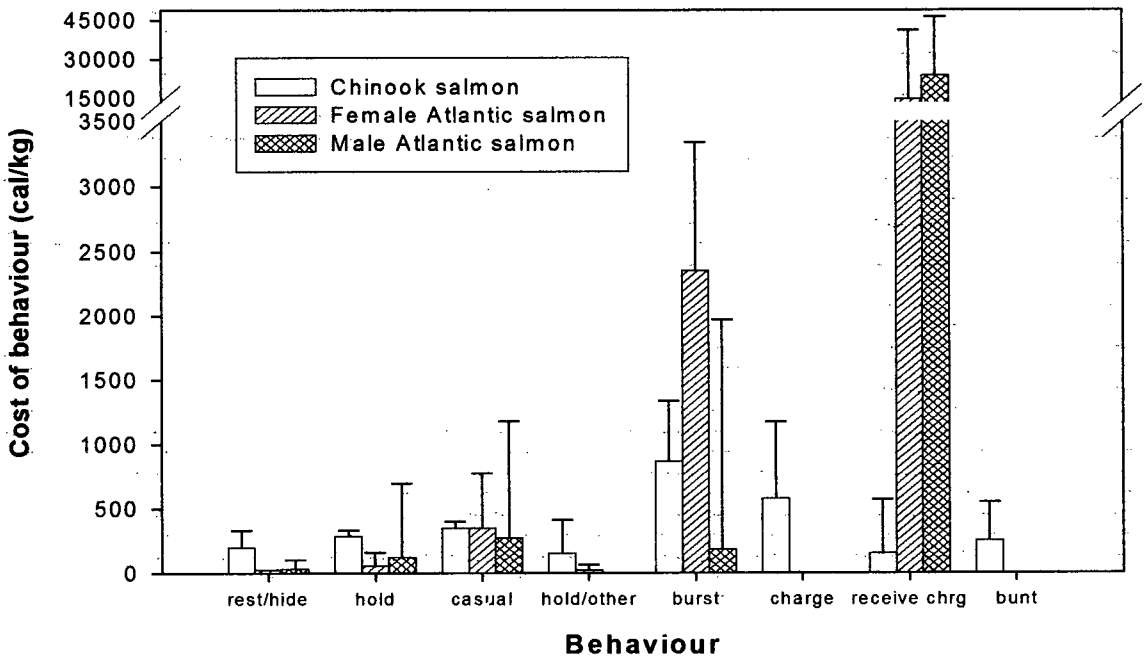

Figure 13: The average energetic cost of each behaviour (cal/kg) for the six Chinook salmon, the four female Atlantic salmon, and the two male Atlantic salmon from Bronte Creek. The error-bars represent 95% confidence limits for the mean of the cost of the individual behaviour.

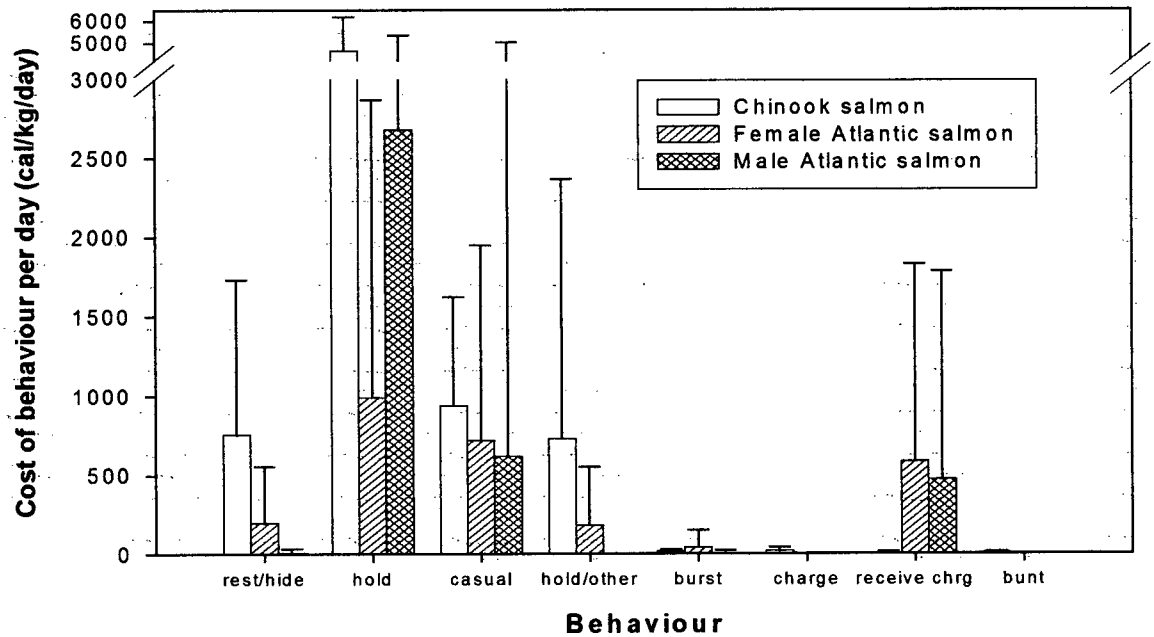

Figure 14: The average daily energetic cost of each behaviour for Chinook salmon and Atlantic salmon. Error-bars represent 95% confidence intervals for the mean of the daily cost of the behaviour. (n=4 female Atlantic salmon, 2 male Atlantic salmon, 5 male Chinook salmon)

All of the energy costs of the behaviours were added together for each species to obtain a daily energy budget (Figure 15). Chinook salmon used the most energy on a daily basis, just over 7000 cal/kg/day. Male Atlantic salmon average daily energy use was 3771 cal/kg/day, higher than the amount of energy used by a female Atlantic salmon, who averaged 2703 cal/kg/day.

As outlined in the introductory section, Atlantic salmon are expected to return to natal rivers earlier in the year than Chinook salmon. After their upstream migration, Chinook salmon may spend 7-15 days on the spawning grounds before spawning, but Atlantic salmon may spend up to two months on the spawning grounds before spawning. However, both species have been recorded to spawn at the same time in the fall and winter. Therefore, in an attempt to get a picture of the total energy expenditure of each species on the spawning grounds in Bronte Creek, the daily energy expenditure for each individual fish was multiplied by the number of days that the fish was tracked and observed. Tracking was stopped (from Table 1) when the carcass of the fish was found or when the frequency reading from the EMG transmitter could not be detected any longer on the spawning grounds and the fish could not be located. Chinook salmon were tracked on the spawning grounds in Bronte Creek for an average of seven days, ranging from four to 12 days and Atlantic salmon were found on the spawning grounds an average of 23 days, ranging from 13 to 38 days. The total energy expenditure of all behaviours for both species for the entire time the fish were on the spawning grounds in Bronte Creek is seen in Figure 16. Chinook salmon used an average of 49,037 cal/kg during their residence on the spawning grounds in Bronte Creek, and Atlantic salmon used an average of 88,712 cal/kg during their residence in Bronte Creek (female Atlantic salmon used an average of 74,111 cal/kg, and male Atlantic salmon used an average of 103,314 cal/kg).

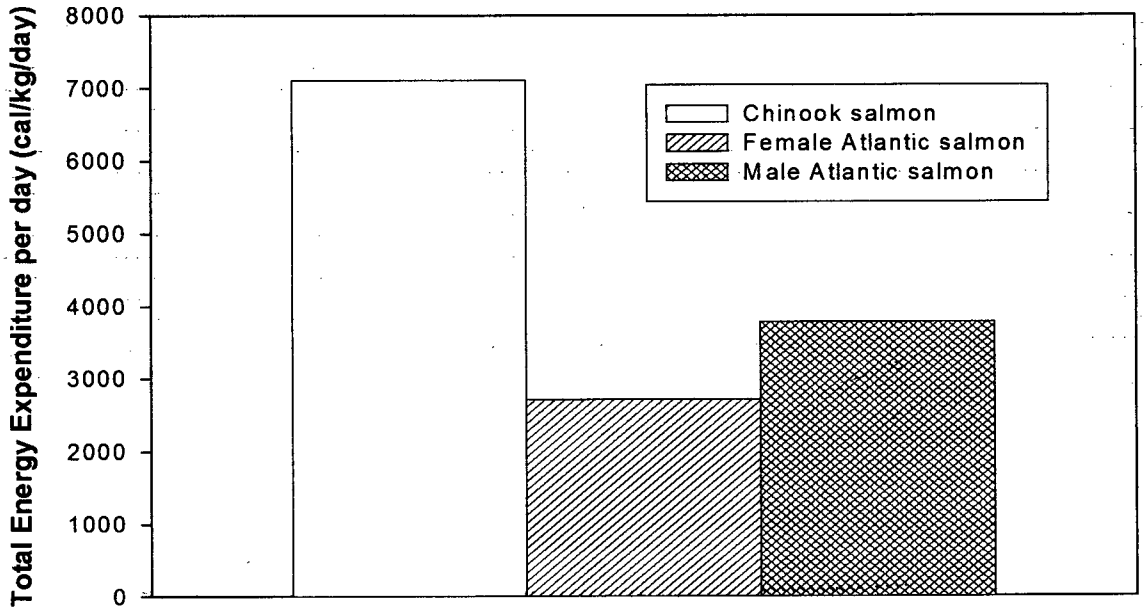

Figure 15: The total daily energy expenditure (cal/kg) of Chinook salmon, male Atlantic salmon and female Atlantic salmon. (n=5 chinook salmon, n=4 female Atlantic salmon, n=2 male Atlantic salmon)

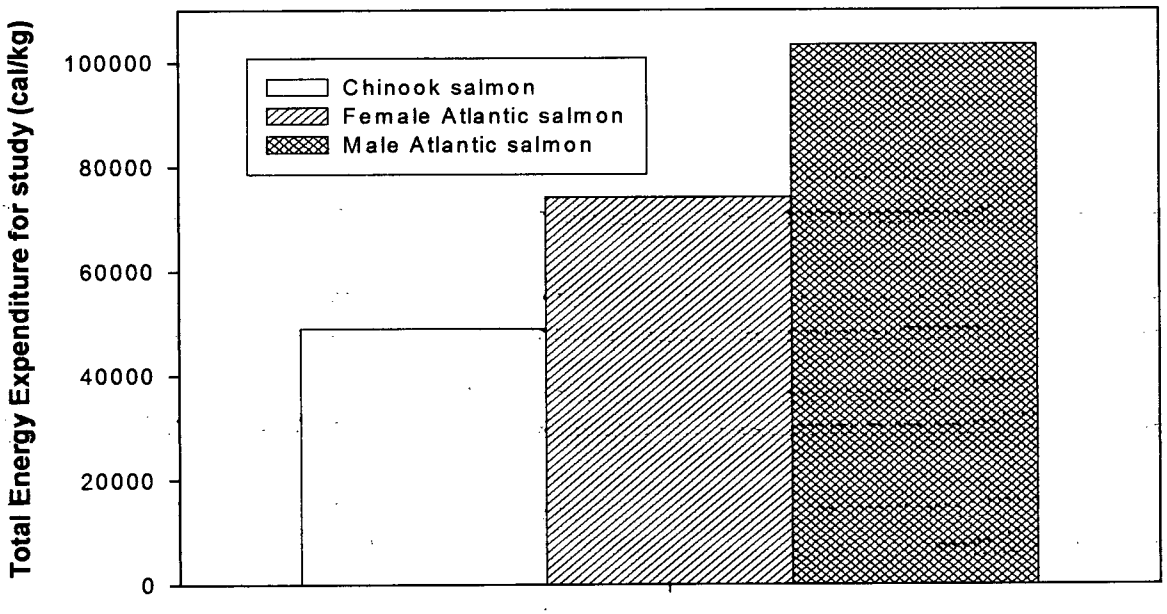

Figure 16: The total energetic cost of all behaviours for Chinook salmon (all male), female Atlantic salmon, and male Atlantic salmon for the total time that the fish were alive in Bronte Creek (Chinook salmon: n=5, t=7 days; Female Atlantic salmon: n=4, t=22 days; Male Atlantic salmon: n=2, t=26 days).

4.0 Discussion

Energy Expenditure

The average daily energy expenditure for the Atlantic salmon in Bronte Creek (3.8 kcal/kg/day for males and 2.7 kcal/kg/day for females) and for Chinook salmon in Bronte Creek (7.09 kcal/kg/day) was similar to that found by Healey *et al.* (2003) for spawning sockeye salmon (*Oncorhynchus nerka*) in Gluskie Creek, British Columbia (5.1 kcal/kg/day for male sockeye and 5.2 kcal/kg/day for female sockeye). From body constituent analysis, average energy expenditures for sockeye salmon and pink salmon (*Oncorhynchus gorbuscha*) in the Adams River, B.C. were calculated to be much higher, however (Brett 1995). Spawning male sockeye salmon used 24 kcal/kg/day and female sockeye used 18 kcal/kg/day. Pink salmon were seen to consume 21 kcal/kg/day and 23 kcal/kg/day for males and females, respectively (Brett 1995).

Hendry and Berg (1999) estimated total energy expenditure of sockeye salmon during spawning from Pick Creek, Alaska, of 1071 kcal for males and 565 kcal for females. Jonsson *et al.* (1991) estimated energy expenditures of Atlantic salmon during spawning from River Imsa, Norway, of 1601 kcal for males and 1086 kcal for females and estimated energy expenditures again in the late 1990's for the same population of 926 kcal for males and 1045 kcal for females (Jonsson and Jonsson 2003). These studies, based on body constituent analysis, report much higher values for energy expenditure than that recorded in my study (263 kcal for male Atlantic salmon, 240 kcal for female Atlantic salmon, and 255 kcal for Chinook salmon) and that reported in Healey *et al.* (2003) for sockeye salmon (117.6 kcal for males and 155.7 kcal for females). However, energy expenditure measured in Pick Creek and in River Imsa are based on a study period of six to eight months longer than that of mine.

The above mentioned studies present energy expenditure values associated with all stages of spawning, including pre-spawning and spent stages. Unfortunately, none of the fish in Bronte Creek spawned. Therefore, energy expenditure values recorded from Atlantic and Chinook salmon in Bronte Creek may have been underestimated in that they do not include energy consumption associated with behaviours of actual spawning. These studies mentioned above, as well as mine, do not include energy expended during migration upstream, prior to spawning. The cost of migration upstream and around physical barriers has been reported for sockeye salmon (Hinch *et al.* 1996) and for other anadromous fish species, including Atlantic salmon and Chinook salmon (Bernatchez and Dodson 1987).

A second reason why total energy expenditure for the fish in Bronte Creek was lower than values reported from previous body constituent analysis studies may be the fact that the fish in Bronte Creek just had less energy to expend. Jonsson and Jonsson (2003) recorded a decrease in energy expenditure from the same population of Atlantic salmon from 1991 to 2003. The Atlantic salmon returned to their natal river with less energy from year to year and so had less energy to spend on spawning in the final year of the study (Jonsson and Jonsson 2003).

Limited rainfall and consequent low water levels during the fall and winter of 2002 in Ontario, along with the fact that fishing is extensive in some areas along Bronte Creek, may have increased stress levels and energy consumption in the Chinook salmon during their limited migration up the creek (Hinch *et al.* 1996). Chinook salmon were blocked at the mouth of Bronte Creek for one to two months before they were transported to the spawning grounds. The Chinook salmon may have used considerable amounts of energy at the mouth of the creek waiting for water levels to rise or trying to get upstream and failing. This may have also had an effect on the resulting total energy expenditure of the fish on the spawning grounds.

The average daily energy expenditure for the Chinook salmon was much higher than that of the Atlantic salmon in Bronte Creek. This may be accounted for by the fact that Chinook salmon were observed to be more active in Bronte Creek than the Atlantic salmon in that they performed the energetically expensive behaviours of charging and bunting more often than the Atlantic salmon. As well, the behaviours of holding and holding with other species were more energetically expensive for the Chinook salmon than for the Atlantic salmon, although male Atlantic salmon and female Atlantic salmon performed the behaviours more often, respectively. The larger daily energy expenditure for the Chinook salmon may also reflect the fact that Chinook salmon are semelparous fish and so there is no need to conserve energy for recovery post spawning as might be the case with the Atlantic salmon, which are iteroparous (Bernatchez and Dodson 1987; Mills 1989; Hendry and Berg 1999). Figure 16 shows that, based on the number of days each species was on the spawning grounds in Bronte Creek, the Atlantic salmon used more energy in total than the Chinook salmon. However, for the limited amount of time that the fish were observed in Bronte Creek, the Chinook salmon used more energy on a daily basis. The Atlantic salmon in Bronte Creek used *twice* as much total energy for the entirety of the study as did the Chinook salmon, but resided on the spawning grounds *three* times longer on average than the Chinook salmon. The low daily energy expenditure by Atlantics may, therefore, be a tactic to conserve energy.

Male Atlantic salmon used more energy on average on a daily basis than the females. Previous studies have found that either the sexes had relatively similar daily energy expenditures (Jonsson *et al.* 1991) or males had much larger daily energy expenditures than females (Hinch and Rand 1998). This is explained in Bronte Creek primarily by the fact that males were

observed holding more often than female Atlantic salmon and this behaviour was more energetically costly for the males. As well, male Atlantic salmon were charged often by male Chinook salmon and "receiving a charge" was energetically expensive. Most female Atlantic salmon seldom received a charge. Unfortunately, no EMG values were recorded for the behaviours of charging and bunting by male Atlantic salmon due to the fact that these behaviours were observed very rarely. Charging and bunting appear to be energetically expensive behaviours for Chinook salmon and so the total daily energy use for male Atlantic salmon may have been underestimated in this study. Male Atlantic salmon were also seen to interact with other male Atlantic salmon more often than the female Atlantic salmon, who spent most of their time alone or interacting with Chinook salmon. Lucas *et al.* (1993) found that female Atlantic salmon heart rate was low when the fish was at rest or moving slowly and high during specific spawning activities, including nest construction. This may reflect the fact that gonad development in females has a higher metabolic cost than that for males (Rand and Hinch 1998). Females are thus at a higher risk of energy exhaustion and so conservation of energy on the spawning grounds may result (Rand and Hinch 1998). Male Atlantic salmon heart rate was continually high throughout the spawning stages (Lucas *et al.* 1993) and this could explain why the male Atlantic salmon consumed more energy than the females in Bronte Creek.

The behaviour of holding by Chinook salmon and Atlantic salmon was by far the greatest daily energy cost of all of the behaviours for both species and this reflects the fact that both species spent most of the day performing this behaviour. Similar daily energy expenditure values were seen for Chinook salmon, which were higher than that of the Atlantic salmon, during casual swimming, resting and/or hiding, and holding next to female Atlantic salmon. These behaviours had higher average energetic costs for Chinook salmon and so the energetic

costs of the behaviours per unit time were also higher than that of the Atlantic salmon, even though the female Atlantic salmon performed the behaviours of resting and/or hiding and holding with other species more often than the Chinook salmon. The remainder of the daily energy expenditure for Chinook salmon behaviours was dedicated to less-costly and less-frequent activities such as charging, bunting, and burst swimming. No EMG values were obtained from either of the species in Bronte Creek for the behaviour of chasing. The addition of chasing would not increase the average daily energy consumption significantly since the frequency of chasing for both species was very low (if it is assumed that chasing has a similar unit time energy cost as burst swimming, then including chasing would add only 7.53 cal/kg to the daily energy budget).

The Atlantic salmon in Bronte Creek, that could be seen and were not hiding under rocks, had similar daily energy costs for casual swimming and for the reaction to receiving a charge. The cost of receiving a charge was high for Atlantic salmon relative to Chinook salmon primarily because the Atlantic salmon were charged at much more often than the Chinook salmon and the specific cost of the behaviour itself was also much higher for Atlantic salmon than Chinook. The small energy cost of receiving a charge for the Chinook salmon was due to a few jacks that were consistently charged by larger male Chinook salmon. All remaining daily energy cost for Atlantic salmon was associated with burst behaviour, which was very small in comparison to other behavioural energy costs.

Male Atlantic salmon were difficult to find in the creek. However, of the fish that could be observed, holding was by far the greatest energy cost of all of the behaviours for both sexes of Atlantic salmon, primarily due to the fact that this behaviour was performed most of the time relative to other behaviours. The male Atlantic salmon were observed to be holding more often than the female Atlantic salmon and thus their average daily energy expenditure for this

behaviour is much larger than that of the female Atlantic salmon. The energy cost associated with casual swimming was similar for male and female Atlantic salmon, but female Atlantic salmon spent more of their daily energy than did males on receiving a charge. This reflects the fact that, although the energetic cost and the frequency of the behaviour was higher for male Atlantic salmon, the one female Atlantic salmon that was charged in Bronte Creek was charged consistently by Chinook salmon and other male Atlantic salmon for the entire 34 days that she was on the spawning grounds, thus increasing the average daily energetic cost of receiving a charge for all female Atlantic salmon. Most female Atlantic salmon spent most of their daily energy expenditure on casual swimming and holding. They were also observed to be resting on rocks or hiding in caves in Bronte Creek more often than male Atlantic salmon and so the consequential daily energetic cost of the resting and/or hiding behaviour is higher for female Atlantic salmon. Both male and female Atlantic salmon only performed the bursting behaviour rarely and so the subsequent energy costs are small. Male Atlantic salmon were never seen to be holding near Chinook salmon so that there was no estimate of cost for this behaviour for males.

Respirometer

The critical swimming speeds calculated for the Atlantic salmon during the respirometer swim trials (62 cm/s to 89 cm/s) were similar to those found by Jain *et al.* (1997) for rainbow trout (*Oncorhynchus mykiss*). Ucrit values for 420-700 g rainbow trout, performing a "ramp test", ranged from 64 cm/s to 87 cm/s (Jain *et al.* 1997). The rainbow trout were swum in a similar tunnel to that used in this study but with a smaller inside diameter of 21 cm. Adult transgenic coho salmon (*Oncorhynchus kisutch*), with an average weight of 2.2 kg, also had similar measured Ucrit values to those in this study, ranging from 61.5 to 72 cm/s (Lee *et al.* 2003a). Ocean-ranched coho salmon of the same size had Ucrit values

between 87.2 and 107.9 cm/s, slightly higher than those measured for the Atlantic salmon in this study. The coho salmon were swum in the same Brett-type respirometer used in this study, but temperatures were a little lower and averaged 8°C (Lee *et al.* 2003a).

Ucrit values obtained from a swim tunnel for sockeye salmon (*Oncorhynchus nerka*) were also similar to those found in this study. Adult sockeye salmon (2.24 kg) had critical swimming speeds ranging from 65.82 cm/s for unhealthy fish and 95.67 cm/s for healthy fish. Unhealthy fish refers to fish that were not treated with chloramine-T to reduce skin lesions and were swam in hypoxia conditions (Jain *et al.* 1998). These fish were swam in a Brett-type respirometer with an inside diameter of 21 cm. Water temperatures during the study ranged from 19 to 21°C, considerably higher than the 12°C average water temperature used for the Atlantic salmon swim trials. Brett and Glass (1973) measured higher critical swimming values for adult wild sockeye salmon however. Ucrit values from 129 to 134 cm/s were recorded for 1.68 kg fish. This study was carried out at 20°C in a larger Brett-type swim tunnel however, with an inside diameter of 28 cm (Brett and Glass 1973). Jain *et al.* (1998) mention that the lower Ucrit values measured in their study, as compared to those measured by Brett and Glass (1973), may be attributed to larger sized fish, as a decrease in relative swimming performance is usually seen with an increase in the size of the fish (Jain *et al.* 1998). As well, Brett and Glass (1973) use a larger swim tunnel and so lower Ucrit values could have been due to limited tailbeat movement of the sockeye in the smaller tunnel (Jain *et al.* 1998).

Mature, Fraser River pink salmon (*Oncorhynchus gorbuscha*) (Fort Langley, BC), averaging 1.59 kg for females and 1.85 kg for males, had higher Ucrit values than those measured for the Atlantic salmon in this study, ranging from 102 cm/s to 105 cm/s for females and from 118 cm/s to 144 cm/s for males (Williams and Brett 1987). The pink salmon were swum in a Brett-type respirometer with an inside diameter of 30 cm, at temperatures ranging

from 10.5 to 12.5°C (Williams and Brett 1987).

Beddow and McKinley (1998 and 1999) reported Ucrit values for Atlantic salmon much higher than those found in this study. The effects of temperature on EMG signals were looked at and Ucrit values for hatchery-reared post-smolts, acclimated for one month at 8°C and 18°C, ranged from 135 cm/s to153 cm/s, respectively. Ucrit values after four months of acclimation ranged from 129 cm/s to 136 cm/s, for 8°C and 18°C, respectively (Beddow and McKinley 1998). Ucrit values at 12°C for hatchery-reared adult Atlantic salmon (0.9 to 2.2 kg) ranged from 140 cm/s to 159 cm/s (Beddow and McKinley 1999). Booth *et al.* (1997) reported Ucrit values of 176 cm/s for adult, wild Atlantic salmon, ranging from 2.5 to 4 kg, at 12°C. These studies on Atlantic salmon used a Blazka-type swim tunnel and no correction for solid blocking was made to the swim speed from Bell and Terhune (1970).

The fish swum in this study were within the range of values observed by other authors but were also in the low end of the range. Although farmed Atlantic salmon do not necessarily show low Ucrit values (see Beddow and McKinley 1999), neither are they exercised to any significant degree in their holding tanks or net pens. They may, therefore, lack the conditioning necessary to sustain high swimming speeds.

While Atlantic salmon energy expenditure was calculated using calibration data from my respirometer trials, Chinook salmon energy expenditures were calculated using an EMG and oxygen consumption relationship from Geist *et al.* (2000). Hinch *et al.* (1996) suggests that EMG and oxygen consumption relationships are sometimes unreliable in measuring energy expenditure as the respirometer may impair fish movement and thus oxygen consumption may be underestimated. However, the respirometer used by Hinch *et al.* (1996) had a diameter of 18 cm, while that used in my study and in Geist *et al.* (2000) were larger tunnels with diameters of

26 cm and 28 cm, respectively. Through visual observations, there was no apparent obstruction to fish movement in the tunnel nor did Geist *et al.* (2000) observe that the Chinook salmon used in his study were restricted by the size of the tunnel. Therefore, I am confident that the oxygen consumption and subsequent energy expenditure calculated for the Chinook salmon and for the Atlantic salmon in this project were not seriously affected by the size of the tunnel.

However, oxygen consumption may indeed be underestimated in that the unidirectional swimming seen in the respirometer is less energetically expensive than spontaneous swimming, including turning and extensive burst swimming (Cooke *et al.* 2000). The consequences of using a respirometer may have underestimated the energy expenditure of either of the species in this study in this respect, and this must be taken into account, however I believe the process is robust enough that reliable results may be obtained and may be comparable to those measured in the field for this study, especially considering the fact that few observations were made of fish bursting in Bronte Creek.

EMG values recorded from Chinook salmon by Geist *et al.* (2000) are similar to those recorded from Chinook in Bronte Creek. There is also a similarity between the EMG values recorded from Atlantic salmon in the swim tunnel in this study and the EMG values recorded from the Atlantic salmon in Bronte Creek. Kaseloo *et al.* (1992) reported similar EMG values to that of this study for adult rainbow trout (average 44 cm long) in a swim tunnel. However, Okland *et al.* (1997) and Beddow and McKinley (1998) reported higher EMG values for wild adult Atlantic salmon in a swim tunnel, and farmed Atlantic salmon smolts in a swim tunnel, respectively. At a swimming speed of 50 cm, an average EMG recording for adult Atlantic salmon in my study was 1350 ms. At the same swimming speed, Kaseloo *et al.* (1992) reported an average EMG value of 1300ms, Okland *et al.* (1997) reported an average EMG value of 1950

ms, and Beddow and McKinley (1998) reported an average EMG value of 1700 ms. These studies were conducted on smaller sized fish than those used in my study. As well, I believe the ranges of EMG values recorded both in the swim tunnel and in Bronte Creek in this study are reliable as the recorded EMG value for a fish at rest (average 1900ms) and a fish burst swimming (average 800 ms) was similar for both Chinook salmon and Atlantic salmon in Bronte Creek and the Atlantic salmon in the swim tunnel. These ranges are also similar to those found by Hinch *et al.* (1996) and Healey *et al.* (2003) for adult sockeye salmon of similar size to the fish in my study.

An exponential curve best described the oxygen consumption ($mgO_2/kg/h$) and swim speed (cm/s) relationship for the Atlantic salmon used in the swim trials in this study. An exponential relationship was also used by Geist *et al.* (2000) for oxygen consumption and swim speed for chinook salmon. However, other studies used a linear regression for this relationship (Brett and Glass 1973; Weatherley *et al.* 1982; McKinley and Power 1992; Cooke *et al.* 2000). McKinley and Power (1992) found that, although the true relationship between oxygen consumption and swim speed is likely exponential, a linear regression is acceptable as the metabolic rate determined for adult lake sturgeon was at the start or "toe" of the exponential curve. At low swim speeds, a linear or exponential curve may adequately describe the results (McKinley and Power 1992).

The oxygen consumption reported for adult lake sturgeon (4-6 kg) at various swim speeds is much lower than that recorded for adult Atlantic salmon in my study (450 $mgO_2/kg/h$ at 50 cm/s). At a swimming speed of 50 cm/s, average oxygen consumption of lake sturgeon, in a swim tunnel with a 30 cm diameter, was measured to be 87 $mgO_2/kg/h$ (McKinley and Power 1992). Cooke *et al.* (2000) also recorded lower oxygen consumption, 130 $mgO_2/kg/h$ at a 50

cm/s swimming speed, for adult rainbow trout (0.8-1.5 kg) in a Blazka-type swim tunnel. Weatherley *et al.* (1982) recorded average oxygen consumption values of smaller sized adult rainbow trout (0.4-0.6 kg) in a Blazka-type swim tunnel, 250 $mgO_2/kg/h$ at a swimming speed of 50 cm/s. The temperature in the swim tunnels for these three studies was similar to that of my study, between 10°C and 12°C, but the swim tunnels used were of much smaller diameter and so may have underestimated oxygen consumption values.

Brett and Glass (1973) recorded oxygen consumption for sockeye salmon smolts (0.005 kg) higher than those found in my study, 800 $mgO_2/kg/h$ at a swimming speed of 50 cm/s. This study was conducted in a swim tunnel with a similar diameter to that of mine (28 cm), but at a temperature of 15°C and with smaller-sized fish. Oxygen consumption increases with increasing temperature and decreasing size (Brett 1973).

Aerobic metabolism and the effect of temperature

Because the electrodes of the EMG transmitter are implanted into the red musculature, a concern exists regarding the underestimation of energy expenditure due to the lack of anaerobic activity measurements. Red muscle in fish is slow and oxidative and has a dense capillary bed, which is associated with a high aerobic capacity for sustained swimming (Beddow and McKinley 1999). White muscle is fast and glycolytic, synthesizing ATP rapidly and providing power for burst swimming. It is known that white muscle is electrically silent at low swimming speeds, but it becomes more active at high speeds and the resulting large EMG (small pulse interval) may be detected by electrodes in the red muscle (Ross *et al.* 1981; McKinley and Power 1992). EMG pulse intervals from the red muscle of both Atlantic and Chinook salmon in Bronte Creek were observed to decrease substantially during burst swimming. Therefore, these results are similar to previous studies that suggest EMG electrodes may be sensitive

to contractions of both muscle types (Ross *et al.* 1981; McKinley and Power 1992; Hinch *et al.* 1996).

Rand and Hinch (1998) found that white muscle recruitment was limited below 80% of the critical swimming speed. Beddow and McKinley (1999) found that white muscle fibres were recruited only at swim speeds greater than 86% Ucrit. The Chinook salmon and Atlantic salmon in Bronte Creek very rarely swam at speeds greater than 80% Ucrit and most energy expended by the fish was through holding or slow swimming and so I believe white muscle recruitment was negligible in my study.

Although the effect of temperature was not specifically measured in this study, it is an important factor that must be taken into account in biological and ecological studies, especially when metabolic rate is involved. Fish are obligate poikilotherms in that, even when they are active, they cannot overcome heat loss through their gills and epidermis and thus their body temperature closely resembles that of the ambient water temperature (Lee *et al.* 2003b). Salmonid species are interesting to study in this respect not only because their niches vary from O°C for Arctic Char (*Salvelinus alpinus*) to 27°C for rainbow trout (*Oncorhynchus mykiss*) (Lee *et al.* 2003b) but as well, an individual salmon must be able to migrate and spawn and complete its life cycle in a range of varying water temperatures.

A change in temperature will have an effect on the metabolic rate of a fish. Oxygen concentration in water increases with decreasing temperature and fish swimming at lower temperatures will have a lower metabolic rate (metabolic processes slow), resulting in decreased oxygen demand (Lee *et al.* 2003b). Lee *et al.* (2003b) reported a 90% increase in oxygen consumption per minute for sockeye and coho salmon from 5°C to 20°C, but reported only a 27% increase in oxygen consumption from 5°C to 10°C. Brett and Glass (1973) reported an

increase in oxygen consumption for adult sockeye salmon of 33% at a swim speed of 20 cm/s from 10°C to 15°C. As swim speed increased the change in oxygen consumption decreased and at 35 cm/s oxygen consumption was only seen to increase 19% with a five degrees increase in temperature (Brett and Glass 1973).

Although the effect of temperature change in my study must be taken into account when calculating average oxygen consumption and subsequent energy expenditures of the fish, the temperature change in Bronte Creek was relatively insignificant over the time of the telemetry studies (about three degrees change) and so the effect of temperature change while on the spawning grounds would have a negligible effect on the total energy expenditure for Chinook salmon and Atlantic salmon measured in Bronte Creek. However, the water temperature of the swim tunnels, used to calibrate energy expenditures, was on average 12°C for both that used in my study and that used by Geist *et al.* (2000). Therefore, based on results reported by Brett and Glass (1973) and Lee *et al.* (2003b), I expect that the total energy expenditure for both fish species in my study was overestimated. However, I believe the effect of temperature had a minimal effect on the results of this study as most of the measurements in Bronte Creek were obtained when the water temperature was between 5 and 6°C. As well, the overestimation of the energy expenditure would not change any comparison between the species.

5.0 Conclusion

Based on visual observations alone, the Chinook salmon were dominant to the Atlantic salmon in Bronte Creek and were much more active in the creek. The Atlantic salmon hid much of the time and showed no signs of challenging the Chinook salmon. Neither species were observed to spawn. Scott *et al.* (2003) observed interactions within and between Atlantic and Chinook salmon during spawning in enclosures constructed in Wilmot Creek, Ontario. Most of the interactions occurred within species, however they found that male Atlantic salmon engaged in more agonistic behaviour when Chinook salmon were present. The Chinook salmon caused a delayed nesting and reduced survival in Atlantic salmon (Scott *et al.* 2003). It is possible that the presence of large male Chinook salmon prevented any spawning by Atlantic salmon in Bronte Creek. Adult Atlantic salmon from the same source have been released into the Credit River, a tributary of Lake Ontario for several years and have spawned successfully there (Fitzsimons *et al.* 1999). Although feral Chinook salmon also spawn in the Credit River they are prevented from coming in contact with the spawning Atlantic salmon by an impassible dam. Thus, the Atlantic salmon used in this study were fully capable of spawning naturally in the wild so that their failure to do so in Bronte Creek must be due to some environmental factor, possibly the presence of aggressive male Chinook salmon.

EMG telemetry proved useful in measuring the energy expenditure of salmon during the pre-spawning stage in Bronte Creek. The average daily energy expenditure of Atlantic salmon in the study was less than that of the Chinook in Bronte Creek and less than that of sockeye salmon recorded in previous studies (Healey *et al.* 2003). This may reflect the fact that Chinook salmon were more active in the creek, but the fact that some behaviours were

energetically more expensive for Chinook salmon than they were for the Atlantic salmon may reflect the iteroparous nature of Atlantic salmon and their long freshwater residency so that they need to conserve energy.

Interactions between species (charging, bunting, chasing) did not contribute much to the total energy budget for either species on the spawning grounds in Bronte Creek. Much of the daily energy budget for all fish in the study was dedicated to holding, resting on the bottom, and to casual swimming. However, inter-specific behaviours such as charging and receiving a charge were energetically expensive and if the frequency of these behaviours were increased, then the total energy budget of either species would also be higher. Salmon in this study rely on energy reserves on the spawning grounds and so an increased energy cost of competitive behaviours may indeed compromise spawning and reproductive success for either species.

Whether or not competitive exclusion is a potential factor between Chinook and Atlantic salmon remains to be seen, but ecological studies such as this are important as the consequences of reproductive failure for salmon extend through the food chain of organisms dependent on salmon. Future studies must involve observations of interactions between the species during spawning and throughout juvenile stages as the life histories of both Atlantic salmon and Chinook salmon are similar in these respects. Future studies may also involve EMG telemetry as a fuller reproductive energy budget may be established from monitoring individuals that actually spawn. As well, further evidence may be obtained regarding the energy cost of interspecific competition by comparing species when alone or when others are present, and clearer evidence may be acquired that the iteroparous species spends less on a daily basis on reproduction than the semelparous species.

Ecological and physiological studies such as this are important in contributing to the fields of fisheries and aquaculture in that they provide insight into the movements and interactive behaviours of farmed fish in the wild. More specifically, in this study, Chinook salmon appear to dominate Atlantic salmon and there does not seem to be a high likelihood of Atlantic salmon being serious competitors to Chinook salmon. One implication of this is that Atlantic salmon will not displace Chinook salmon in B.C. rivers. Studies such as this must continue in order to further identify specific influences aquaculture may have on the environment. In this way, procedures may be taken through management strategies to ensure that the field of aquaculture and its future are environmentally sustainable.

6.0 References

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