

**Adaptation and habitat selection during the migration of an  
Arctic anadromous fish, Broad Whitefish (*Coregonus nasus*  
(Pallas 1776))**

by

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## **ABSTRACT**

Broad Whitefish are an anadromous Arctic fish species in the Mackenzie River Valley, N.W.T. that undergo extensive spawning migrations to spawning grounds located on tributaries of the Mackenzie River, like the Arctic Red River. These spawning migrations occur annually between mid-October and early November as demonstrated with catch-per-unit-effort. The maturity stage development of Broad Whitefish is can be predicted by using the variables by gonad-weight and timing of migration for both female and male Broad Whitefish; however, male Broad Whitefish maturity stage also requires the variable abundance for prediction. At the time of Broad Whitefish migration the river environment has slow flowing water as documented by current profiles. The water velocity speeds present in the river at the time of migration are not a barrier to Broad Whitefish migration as Broad Whitefish can swim against water velocities 4 to 10 times higher. This research contributes important life history, migrating characteristic and swimming ability information to the knowledge of Broad Whitefish in the Mackenzie River System.

## **DEDICATION**

I dedicate this thesis work to my parents Caroline and Steve Pawlychyn who instilled in me the love and query of nature at a young age along with the desire to answer those queries.

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## Chapter 1: Literature Review

### *Habitat Selection*

To persist, an organism must successfully complete each stage of its life cycle. Adaptations to effectively use available habitat will influence the organism's life history during its life cycle (Miller and Brannon 1981). How well a habitat meets the needs of the individual during each stage in the life cycle will affect the fitness and survival of the individual. Habitats that meet all the needs of an organism will result in increased fitness and survival for the organism. All organisms seek optimal habitats for critical life history stages. Fish require suitable reproductive habitats and favourable ecological conditions for their young. In later life stages, fish require habitats that maximize growth and maturation (Miller and Brannon 1981, Stearns 1993). As well, fish may require appropriate refugia to maintain themselves during periods of harsh environmental conditions. For example, during the winter in Arctic regions, fish must find deep lakes that do not freeze to the bottom (Wrona *et al.* 2005).

The environmental needs of an organism at each stage in the life cycle may differ. For example, fish eggs require regularly flowing water with moderate to light water velocity (to decrease fungal growth) and high oxygen concentration (10 mg/L or higher) (Hynes 1972, Quinn 2005, Louhi *et al.* 2008). There are many biological threats to fish eggs, including: predators, and bacterial and fungal infections. Thus many fishes, like Pacific salmon, will migrate long distances to reach spawning areas (usually in the headwaters of rivers) of flowing water with high oxygen content and little biological activity (Hynes 1972). While fish eggs require environments of low biological activity, this is typically not ideal for larvae that require large abundance of a specific food (e.g.

plankton blooms) (Healey 1979, James *et al.* 2003). Furthermore, the adult stage of the same species will require more habitat space and, usually, a different food source (Metcalf *et al.* 2002). It is important to recognize that only the juvenile and adult life stages have the potential to actively migrate, while larvae can only passively migrate. Eggs are generally sedentary, although Northcote (1982) notes that even eggs may move in some cases. For example, the Goldeye (*Hiodon alosoides*), the Shad (*Hilsa ilisha*), and the African cyprinid (*Labeo victoriarior*) lay semi-buoyant eggs that drift downstream to a more appropriate habitat for emergence (Northcote 1982). In contrast, many species have non-buoyant eggs that do not move (e.g. Eulachon (*Thaleichthys pacificus*) and some coregonids). These eggs may possess an adhesive substance aiding to hold the eggs in place (Mansueti 1964, Yi *et al.* 2010), or the eggs may be buried, as is common practice within the salmonid family (Quinn 2005). The female salmonid typically buries her eggs in a gravel nest, or on top of gravel substrate (Scott and Crossman 1973). Eggs which remain sedentary require that the habitat they are placed in by the adult must meet all of their needs, for example, temperature, oxygen concentration, and sufficient predation protection and/or camouflage (Quinn 2005).

For most species there is no one habitat that will meet the needs of all stages in the life cycle (Northcote 1982). Therefore, movement between two or more habitats over a life cycle is often necessary (Brannon 1981). This movement from one vital habitat (e.g. feeding area) to another vital habitat (e.g. spawning ground) is called migration (Roff 1992). Migration has evolved in response to the variable nature of the different habitats, in which larvae and/or adults reside (Dingle 1985).

## *Fish Migration*

Fish migrations have predictable routes and predictable timing (e.g. seasonally), depending on a fish's life stage (Brannon 1981, Roff 1992). This predictable spatial-temporal migration is theorized to place individuals in the most optimal habitat at the most optimal time, based on assumptions that ancestral environmental knowledge (evolutionary adaptation) is passed from generation to generation and that the environment used remains constant (Brannon 1981). Miller and Brannon (1981) describe the predictability of fish migration as utilizing "time-windows". These time-windows allow individual fish that have successfully completed the precursory stage(s), such as emerging at the correct time, to drift downstream to the desired location for the purpose of utilizing critical resources within the 'new' habitat (e.g. larval fishes are at the right place at the right time to feed on plankton) (Miller and Brannon 1981).

Time-windows are spatio-temporal (Miller and Brannon 1981) and critical to survival. For example, the time-window of spawning is essential for emergence of the larvae at the correct time, in the correct place (Miller and Brannon 1981). If eggs are not placed in the right habitat at the right time, the fitness of the eggs may decline. If the environment of the eggs is too hot or too cold, the consequence may be reduced fitness of the emerging larvae, resulting in poor health/increased likelihood of disease upon emergence, or emergence mal-timed with food availability (Miller and Brannon 1981).

Sinclair (1988) noted that the richness of a population is defined by the number and location of habitats within which a species life cycle can be completed. The population richness of a species may be determined by the success of early life-history stages, when the diversity of populations within a species is correlated to the number of

optimal larval retention areas (Sinclair 1988). For example, multiple populations of American Shad (*Alosa sapidissima*) may be associated with different spawning grounds within a river, whereas Mackerel (*Scomber japonicus*) populations have been correlated to two egg and larvae retention areas within their ocean habitat (Sinclair 1988). Thus, American Shad are more population rich than Mackerel. Notably, even though the adult stages of the Mackerel populations inter-disperse, the egg and larvae stages do not due to the geographically separated spawning grounds thus isolating the distinct populations (Sinclair 1988).

McDowall (1997) classified migratory patterns of fishes into three types: oceanodromy, potamodromy and diadromy. Oceanodromy refers to fish migrations isolated within saltwater environments (Moyle and Cech 2004). Potamodromy indicates fish migrations isolated to freshwater habitats (McDowall 1997). Diadromous fish migrate between saltwater and freshwater habitats (Moyle and Cech 2004).

#### *Migration Patterns - Anadromy*

There are three common diadromous migration patterns: catadromy, amphidromy and anadromy (McDowall 1997). Catadromous fish spend the majority of their life cycle in freshwater and only use saltwater for spawning (Cullen and McCarthy 2003), with the exception of the American Eel (*Anguilla rostrata*) and the European Eel (*Anguilla anguilla*) who's life cycle involves juveniles remaining in freshwater for 2-3 years before migrating into saltwater (Moyle and Cech 2004). Amphidromous fish migrate between saltwater and freshwater environments for purposes other than spawning, such as feeding (Arnold 1981), or predator avoidance. Anadromous fish divide their life cycle between



saltwater and freshwater, experiencing most of their growth in saltwater habitats, but returning to freshwater for reproduction and spawning (Moyle and Cech 2004). In saltwater, anadromous fish have increased food sources allowing them to grow and acquire the necessary energy for sexual maturation (Foerster 1968). To be able to transition from freshwater to saltwater, diadromous fishes must alter their ion-regulatory abilities; this is typically done via ontogenic changes mediated by hormones (Moyle and Cech 2004). Many species, like Pacific salmon, live the majority of their lives in saltwater and are only in freshwater at the very beginning and very end of their lives (Quinn 2005).

Many anadromous fishes travel extensive distances to reach spawning and feeding grounds (McDowell 1997, VanGerwen-Toyne *et al.* 2008) (Table 1). Anadromous spawning migrations are physically demanding and, therefore, energetically expensive. Spawning sites are typically upstream of feeding sites (Brannon 1981, Miller and Brannon 1981, Northcote 1982, Reist and Chang-Kue 1997), increasing the cost of migration. Many species cease to feed completely once they reach freshwater (Brannon 1981, Metcalfe *et al.* 2002). For anadromous migrations to persist there must be sufficient benefits to gain (Alexander 1998). Regardless of the cost, as previously mentioned, a large number of species do migrate. Anadromy is the predominant life history pattern of many fishes that live in cool-temperate and sub-polar to polar waters, where ocean productivity surpasses freshwater productivity (Gross *et al.* 1988, Metcalfe *et al.* 2002). The cost of such migrations is an evolutionary ‘trade-off’ for favourable spawning grounds (Moyle and Cech 2004), increased egg survivorship and larval fitness (Brannon 1981). The advantages of migrations are: 1) increased probability of larval stages

Table 1: Spawning migration timing, type, behaviour and species distribution of common Arctic fish species in North America.

<b>Species</b>	<b>Latin name</b>	<b>Migration timing to spawning location</b>	<b>Spawning timing</b>	<b>Migration behaviour</b>	<b>Region</b>	<b>Distance of migration to spawning grounds</b>	<b>Reference</b>
Atlantic Salmon	<i>Salmo salar</i>	Fall (Months)	Fall (October to January)	Anadromous	Eastern Arctic	24 – 300 km	Finstad <i>et al.</i> 2005, Kottelat and Freyhof 2007
Sockeye Salmon	<i>Oncorhynchus nerka</i>	Summer (Months)	Fall	Anadromous	West – Fraser River	400 - 1100 km	Killick 1955, Hinch and Rand 1998, Quinn 2005
Arctic Charr	<i>Salvelinus alpinus</i>	Late summer to fall (Months)	Fall (September and October)	Anadromous	West and East	300 - 940 km	Hatfield <i>et al.</i> 1972, Kottelat and Freyhof 2007
Arctic Grayling	<i>Thymallus arcticus</i>	Spring (Months)	Spring (May to June)	Lake to River River to river	West and Central	69 – 72 km	Hatfield <i>et al.</i> 1972, Craig and Poulin 1975, Falk <i>et al.</i> 1982, Northcote 1993, Kottelat and Freyhof 2007
Arctic Lamprey	<i>Lampetra japonica</i>	Spring (May to July)	Spring	Anadromous	Western Arctic	Long distances >20km	McPhail and Lindsey 1970, Hatfield <i>et al.</i> 1972, Nursall and Buchwald 1972, Scott and Crossman 1973
Dolly Varden	<i>Salvelinus malma</i>	Fall (August to September)	Fall (September to November)	Anadromous	Western Arctic	>130 km	McPhail and Lindsey 1970, Hatfield <i>et al.</i> 1972, Scott and Crossman 1973, Sandstrom <i>et al.</i> 2009
Inconnu	<i>Stenodus leucichthys nelma</i>	Summer (July and August)	Fall (September and October)	Anadromous Semi-Anadromous	Western Arctic	Up to 1500 km	Hatfield <i>et al.</i> 1972, Alt 1977, Howland <i>et al.</i> 2000, 2001, Kottelat and Freyhof 2007

Table 1 continued: Spawning migration timing, type, behaviour and species distribution of common Arctic fish species in North America.

Lake Whitefish	<i>Coregonus clupeaformis</i>	Fall (September to October)	Fall (September to December)	Anadromous	Western and Central Arctic	180 – 480 km	Hatfield <i>et al.</i> 1972, Howland <i>et al.</i> 2009
Broad Whitefish	<i>Coregonus nasus</i>	Summer and Fall (July to October)	Fall (October and November)	Anadromous Lacustrine	Western Arctic	350 – 640 km	Hatfield <i>et al.</i> 1972, Chang-Kue and Jessop 1991, Tallman <i>et al.</i> 2002, Howland <i>et al.</i> 2009
Arctic Cisco	<i>Coregonus autumnalis</i>	Summer (Months)	Summer and early autumn	Anadromous	Western Arctic	1500 km	McPhail and Lindsey 1970, Hatfield <i>et al.</i> 1972, Scott and Crossman 1973, Kottelat and Freyhof 2007
Least Cisco	<i>Coregonus sardinella</i>	Summer to Fall (June to September)	Fall (September and October)	Lacustrine Semi-Anadromous	Western Arctic	800 – 1000 km	Hatfield <i>et al.</i> 1972, Scott and Crossman 1973, Kottelat and Freyhof 2007
Northern Pike	<i>Esox lucius</i>	Spring (April to June)	Spring (April to June)	Fluvial	Western, Central and Eastern Arctic	1.9 km	Hatfield <i>et al.</i> 1972, Scott and Crossman 1973, Jessop and Lilly 1975, Rosell and MacOscar 2002, Kottelat and Freyhof 2007
Burbot	<i>Lota lota</i>	Late fall to winter (September to December)	Mid-winter (January to March)	Freshwater	Western, Central and Eastern Arctic	40 – 280 km	Hatfield <i>et al.</i> 1972, Scott and Crossman 1973, McPhail 1997, Slavik and Bartos 2002, Kottelat and Freyhof 2007

reaching feeding grounds, 2) decreased probability of intraspecific competition for resources among age classes (Moyle and Cech 2004), 3) each life stage develops in an optimal habitat (Miller and Brannon 1981, Brannon 1981) and 4) decreased possibility of cannibalism (Moyle and Cech 2004).

### *Reproductive Behaviour*

Semelparous, compared to iteroparous (perennial), reproduction has a profound effect on migratory strategies. Semelparity refers to one reproductive event per lifetime (Stearns 1993). Good examples and well studied semelparous species include some of the Pacific salmon family, Chum Salmon (*Oncorhynchus keta*) (Tallman 1988), Pink Salmon (*Oncorhynchus gorbuscha*), Coho Salmon (*Oncorhynchus kisutch*) (Scott and Crossman 1973, Quinn 2005), and Chinook Salmon (*Oncorhynchus tshawytscha*) (Keefer *et al.* 2004), and all lampreys for example, American Brook Lamprey (*Lampetra appendix*), Sea Lamprey (*Petromyzon marinus*) (Andrade *et al.* 2007), Northern Brook Lamprey (*Ichthyomyzon fossor*), (Scott and Crossman 1973) and Pacific Lamprey (*Lampetra tridentata*) (Farlinger and Beamish 1984, Keefer *et al.* 2009). Iteroparity refers to more than one reproductive event per lifetime (Stearns 1993), common among most fish species (Moyle and Cech 2004). Murphy (1968) examined the correlation between reproductive pattern and environmental variability, postulating that, in a deterministic and steady environment (such as the North Pacific Ocean), semelparity will result in higher survivorship. In contrast, variable environments such as the Arctic favour iteroparity (Roff 1992).

Leggett and Carscadden (1978) demonstrated that the reproductive behaviour of American Shad fluctuated with the latitude of the spawning river. Southern populations were completely semelparous, while northern populations were 55% to 77% iteroparous (Leggett and Carscadden 1978). The northern populations had lower fecundity than the southern populations when

comparing a single spawning event. This allowed the northern populations to conserve energy for post-spawning survival. Northern spawning rivers were classified as harsher and more variable environments, favouring the reproductive strategy of “bet-hedging”, or iteroparity (Leggett and Carscadden 1978).

Semelparous species invest more into a single reproductive event than iteroparous species (Roff 1992). This results in earlier maturation (Stearns 1993), higher fecundity, and larger egg size in semelparous individuals (Moyle and Cech 2004). Iteroparous species require energy for post-spawning survival, so less energy is allocated into each single spawning event (Roff 1992) and the individuals mature later in life (Stearns 1993). Glebe and Leggett (1981) found that there was a significant difference in the energy allocation per spawning event to the gonads of semelparous and iteroparous populations of American Shad. The iteroparous individuals consumed less than 60% of their total energy reserves during migration and spawning whereas the semelparous individuals allocated more than 70% of their total energy reserves during migration and spawning (Glebe and Leggett 1981).

The ratio between iteroparity and semelparity decreases with the rate of annual reproduction and increasing adult survivorship. This means high adult survivorship and a low rate of reproduction will tend to shift the selective advantage towards iteroparity (Roff 1992). If a population has high adult survivorship and is stationary (stationary is defined as a population in which the number of individuals remains constant over time), to have equal fitness the semelparous life history will require ten times the reproductive productivity (number of offspring) of the iteroparous life history (Roff 1992). When hormonally controlled semelparous individuals do not reproduce (e.g. castrated salmon (Robertson 1961) and octopus with the optic gland removed (Wodinsky 1977)), they live longer by allocating energy for growth and repair instead of reproduction (Stearns 1993).

Cole (1954) introduced a model that assessed the fitness of different reproductive strategies – Cole’s Paradox. Cole determined that annual (semelparous) spawners needed to produce one more offspring in their clutch to equal the fitness of a perennial (iteroparous) spawner. Why, then, would any animal be iteroparous (Stearns 1993)? Charnov and Schaffer (1973) and Young (1990) revisited Cole’s Paradox theory and realized that the model omitted mortality rate, a critical parameter in life history models. Charnov and Schaffer (1973) determined that semelparity will result in greater fitness when adult mortality rates are greater than juvenile mortality rates. In contrast, iteroparity will result in higher fitness when adult mortality rates are lower than juvenile mortality rates. Young’s (1990) research produced similar results; any change in fecundity, age-at-maturity, or age-specific mortality that reduces juvenile survival and increases adult survival will increase iteroparic fitness and decrease semelparic fitness.

### *River Migration*

During migration, anadromous fishes must migrate in freshwater rivers, which offer a unique challenge to migration. Rivers, for the most part, are characterized by unidirectional flow with intermittent, short-term and small back eddies (Hynes 1972). Movement of fishes within a river is limited by the volume of water, depth limits vertical movements of fish, and width limits side to side movement of fish (Northcote 1982).

Rivers offer a wide range of habitats, due to their natural branching (Northcote 1982). The habitat and environmental characteristics of a river system can be very dynamic, changing from branch to branch and from upstream to downstream (Northcote 1982). Rivers exhibit more temporal variation than oceanic and coastal environments. For example, river discharge can change year to year, and river turbidity and temperature can change daily (Northcote 1982).

Spatial changes over the length of a river are predictable and have been modeled as the River Continuum Concept (RCC). The RCC states that the physical, chemical, and biological attributes of a river change with stream order size, which increases from the headwaters towards the mouth (Mackie 2004). The upper reaches of a stream (stream order 1 - 3) are typically narrow, well shaded by riparian canopy, with cold water, and high oxygen concentrations (Cushing and Allan 2001). The mid-reaches of a river (stream order 4 - 6) are characterized as being wider, containing high nutrient levels and warmer water (Cushing and Allan 2001, Mackie 2004). The lower reaches of a river (stream order 7 and up) are typically wide, deep, and slow flowing with high turbidity (Mackie 2004). Due to habitat diversity throughout the river reaches, different fish stages (e.g. larval and adult) inhabit appropriate niches within the same river system. In addition, different fish species occupy different reaches of the river, adding to the aquatic diversity of species within a river (Mackie 2004).

### *Arctic Environment*

The Arctic is characterized by the following: extreme variation in climate and weather (Wrona *et al.* 2005), low amount or absence of sunlight in winter, long days (almost 24 hour sunlight) during the summer (McBean 2005), the prevalence of permafrost over large areas and the persistence of seasonal ice and snow cover (Wrona *et al.* 2005). The Arctic characteristically exhibits extreme seasonality and severe temperature extremes (Wrona *et al.* 2005). Arctic winters have a mean temperature of  $-20^{\circ}\text{C}$ , with record lows of  $-88^{\circ}\text{C}$  (Przybylak 2003). Arctic summer temperatures range from  $-4^{\circ}\text{C}$  near the North Pole to  $+32^{\circ}\text{C}$  along the Mackenzie River Valley. In addition, the Arctic has high intra- and inter-annual variability in temperature and precipitation and seasonally driven latitudinal gradients of solar and UV radiation levels (Wrona *et al.* 2005).

Some of the largest rivers in the world are in the Arctic (e.g. Lena River in Siberia and Mackenzie River in Canada) along with many smaller permanent and semi-permanent streams and rivers (Wrona *et al.* 2005). The variability and dynamics of the Arctic climate produce four hydrological periods in Arctic freshwater habitats: snow melt, outflow at spring break-up, ice-free summer, and ice-covered winter (Pielou 1994). Spring break-up and outflow can last days to weeks and accounts for 75% of the total annual flow. The ice-free summer is characterized by extended sunlight exposure, causing high evaporation rates. Lastly, the ice-covered winter is characterized by cold water temperatures (near 0°C) and high ice accumulation, often more than two meters thick on lakes (McBean 2005), due to limited or no sunlight exposure (Wrona *et al.* 2005).

The nature and severity of climate and weather have strongly influenced the hydrology and consequently the ecology of Arctic freshwater systems (Pielou 1994). Despite the extreme and difficult environmental conditions, Arctic freshwater systems contain a wide diversity of organisms that have adapted to Arctic environments (Wrona *et al.* 2005). For example, organisms have developed one or several of the following adaptations: resting stages (e.g. fish who rest for at least one year between spawning periods), physiologically adaptation to cold water, adaptation with migration and/or some organisms have adapted the ability to grow and reproduce quickly during brief growing seasons (Wohlschlag 1960, Wrona *et al.* 2005, Siikavuopio *et al.* 2009). The environmental extremes of the Arctic result in overall low annual productivity in freshwater (Murray 1998) leading to slower growth and longer-lived species. These unique adaptations allow many organisms to thrive in the Arctic (Wrona *et al.* 2005).

For fish species in the Arctic, migratory behaviour is a common adaptation with anadromy being most common (Wrona *et al.* 2005). The distribution of anadromous fish species is strongly



influenced either directly or indirectly by climatic variables, temperature in particular (Wrona *et al.* 2005).

Despite the climate and environmental challenges, the Arctic is home to approximately 100 species in 48 genera of freshwater and diadromous fish. The unglaciated Beringia and the western Canadian Arctic region are home to 58 named taxa (Wrona *et al.* 2005). Reist (1994) defined an Arctic Guild of freshwater fishes as species distributed entirely or predominantly in northern regions, adapted to cold water temperature ( $<10^{\circ}\text{C}$ ), short growing seasons, extensive ice presence, and long periods of darkness. Species from the Arctic Guild include Broad Whitefish (*Coregonus nasus*), Arctic Cisco (*Coregonus autumnalis*) and Arctic Char (*Salvelinus alpinus*) (Reist 1994).

#### *Influence of Ice on Migration*

Arctic rivers are ice covered for most of the year; consequently, it is critical to consider the impact of ice on migration. The whole mass (water) of a river needs to cool close to  $0^{\circ}\text{C}$  before considerable amounts of ice will form (Hynes 1972); this is because warmer water increases turbulence which mixes the water, inhibiting ice formation (Hynes 1972). Ice acts as an insulator keeping water under the ice warmer than ambient air. The water under the ice may remain fluid while ambient air temperatures drop to  $-50^{\circ}\text{C}$  or below. Ice also acts as a barrier, reducing oxygen transfer from ambient air into the water (Hynes 1972). In southern parts of North America, rivers flow southerly. Ice formation on these rivers starts at the headwaters and develops downstream to the mouth of the river. In contrast, rivers in the Arctic, such as the Mackenzie River, flow northerly. The ice in these rivers starts to form at the mouth of the river and develops upstream towards the headwaters, thus often causing temporary backup of water at the southern end (Lawford 1994). The southerly extent of backup fluctuates year to year. For any ice that has developed on smaller tributaries (e.g. the Arctic Red River), the backup will cause the ice already

formed to lift and separate from the bank. The backed-up water then rises laterally up the banks. Ice formation or break-up on a river significantly increases the uncertainty in absolute values of the flow measurements, especially in the Arctic (Gray and Prowse 1992, Belatos *et al.* 1993, Lawford 1994). The unique formation of ice on Arctic rivers is another environmental characteristic that fishes must adapt to.

In addition to surface ice formation, there are two forms of underwater ice formation: frazil ice and anchor ice. Both increase friction in water, can cause a river to slow dramatically and reduce available habitat to fish (Mackie 2004). Frazil ice is the formation of crystals within the water column (typically starting along the surface) when water is supercooled (Belatos *et al.* 1993). This process occurs in shallow and deep water and can form incredibly thick ice (Hynes 1972, Mackie 2004). Anchor ice is ice that develops on the substrate of rivers (Belatos *et al.* 1993). Anchor ice begins to form on riffles on the upstream side of objects and may spread downward and away from the shore (Hynes 1972). Anchor ice tends to form overnight and may detach and flow downstream during the day (Mackie 2004). The presence of anchor ice can cause the discharge at night to be half that of the discharge during the day (Mackie 2004).

Ice significantly influences habitat use by freshwater fishes (Hynes 1972) as frazil ice may limit available habitat from the surface and anchor ice may limit available habitat from the bottom of a river (Belatos *et al.* 1993). This often results in habitat loss as the presence of hanging frazil ice (ice dams) and anchor ice physically reduces the available habitat to fish (Belatos *et al.* 1993, Komadina-Douthwright *et al.* 1997). The reduction of available winter habitat (Wrona *et al.* 2005), may force many fish to migrate to other areas in the aquatic system, or to move into deeper areas in lakes (Hynes 1972).

## *Mackenzie River*

The Mackenzie River, located in the Northwest Territories of Canada, is one of the world's largest river systems (Mackenzie River Basin Study Report 1981). The Mackenzie River flows northward from Great Slave Lake to the Arctic Ocean and has headwaters in the Yukon, northern British Columbia, Alberta, and Saskatchewan (Stein *et al.* 1973). The Mackenzie River Basin harbours three major lakes, two significant freshwater deltas, and the world's tenth-largest marine delta (Mackenzie River Basin Study Report 1981). The total distance from furthest headwater to the Arctic Ocean is 4,321 km (2,685 miles) (Stein *et al.* 1973, Lawford 1994).

There are two climates within the Mackenzie River basin: tundra in the northeast region and sub-Arctic everywhere else. Characteristically, these climates are dry, with low precipitation (Pielou 1994) and cool summers (Mackenzie River Basin Study Report 1981). Typical of Arctic environments, the northern region of the Mackenzie River Basin (north of the 60<sup>th</sup> parallel) has very cold, long winters with temperatures as low as -50°C at night and cold spells of below -40°C lasting for several weeks at a time (Mackenzie River Basin Study Report 1981). From February to March the sun's position relative to the earth moves northward (this is a result of the tilt of the earth's axis and how that tilt affects the relative position of the sun in the sky over different parts of the earth while the earth rotates around the sun); this results in an increase in ambient temperature and decrease in atmospheric pressure, thus starting the snowmelt. In the northern reaches, ice cover begins around September, compared to the south, where ice cover begins mid-November. In the northern reaches, most of the ice cover is melted by late June. In the south, ice cover melts in late April (Mackenzie River Basin Study Report 1981, Thera 1998).

The melting of ice cover results in the opening of summer habitats for freshwater fishes. Spring break-up of the Mackenzie River is the major hydrological event of the year, characterized

by high water levels, increased water velocity, and increased erosion of the river channel (Hynes 1972, Lawford 1994).

The freshwater Mackenzie River plume runs northward and as it enters the Beaufort Sea it is deflected northeastwardly across the outer delta and along the coast of the Tuktoyaktuk Peninsula by generalized storm tracks from the west and the Coriolis Effect (Reist and Bond 1988). This freshwater influx provides a large area of freshwater habitat extending across the delta, which migrating fishes utilize during all life history stages (Reist and Bond 1988, Thera 1998). In contrast, the nearshore area west of the Mackenzie River Delta remains highly saline (Thera 1998), influencing the distribution of anadromous fishes, like Broad Whitefish, westward into the freshened water along the coast of the Tuktoyaktuk Peninsula (Reist and Bond 1988). The Tuktoyaktuk Peninsula, Richard's Island, and some areas of the outer delta which contain freshwater lakes, are important juvenile rearing grounds for anadromous fish species (Lawrence *et al.* 1984, Bond and Erickson 1985, Bodaly *et al.* 1989, Chang-Kue and Jessop 1992). These lakes have summer water temperatures reaching 18.5°C and high benthos and plankton productivity providing good growing conditions for juvenile fishes. These lakes are connected to saline habitats from summer to fall by streams which are used for migration by fish, these streams freeze completely during winter isolating the lakes from saline habitats (Bond and Erickson 1985).

### *Arctic Red River*

The Arctic Red River (Figure 1) is one of several large tributaries of the Mackenzie River in the Northwest Territories. It originates from a glacier and flows north-northwest through the Mackenzie mountain range, through a canyon and valley system, up and over the Peel plateau before widening, slowing, and reaching the Mackenzie River (Lloyd 1943, Tallman *et al.* 2002). The Arctic Red River is approximately 450 km long, with channel widths ranging from 200 (upstream) to 500 (at the mouth) meters across and depths up to ten meters (Howland 1997). Water discharge levels from the Arctic Red River fluctuate greatly over the year, with peak discharge months (approximately 2000 m<sup>3</sup>/s) during the summer and fall (May – September) and a drastic drop off in discharge (< 200 m<sup>3</sup>/s) occurring in late fall to early winter (October – November) (Environment Canada, Water Survey). It is important to note that the timing of whitefish spawning migration coincides with the drastic decline in water discharge (Change-Kue and Jessop 1992; Howland 1997). This decline may be due to decreased input of flow from the mountainous regions upstream (Pielou 1994), to frazil ice development and/or water back-flowing (Lawford 1994). As noted, fish migrations coincide with the water discharge decline in the Arctic Red River. The habitat available to migrating fish under the ice has not been assessed. It is one of the objectives of this research to determine the natural environment within the Arctic Red River during the time of whitefish migration and to assess how this may or may not affect whitefish migration.

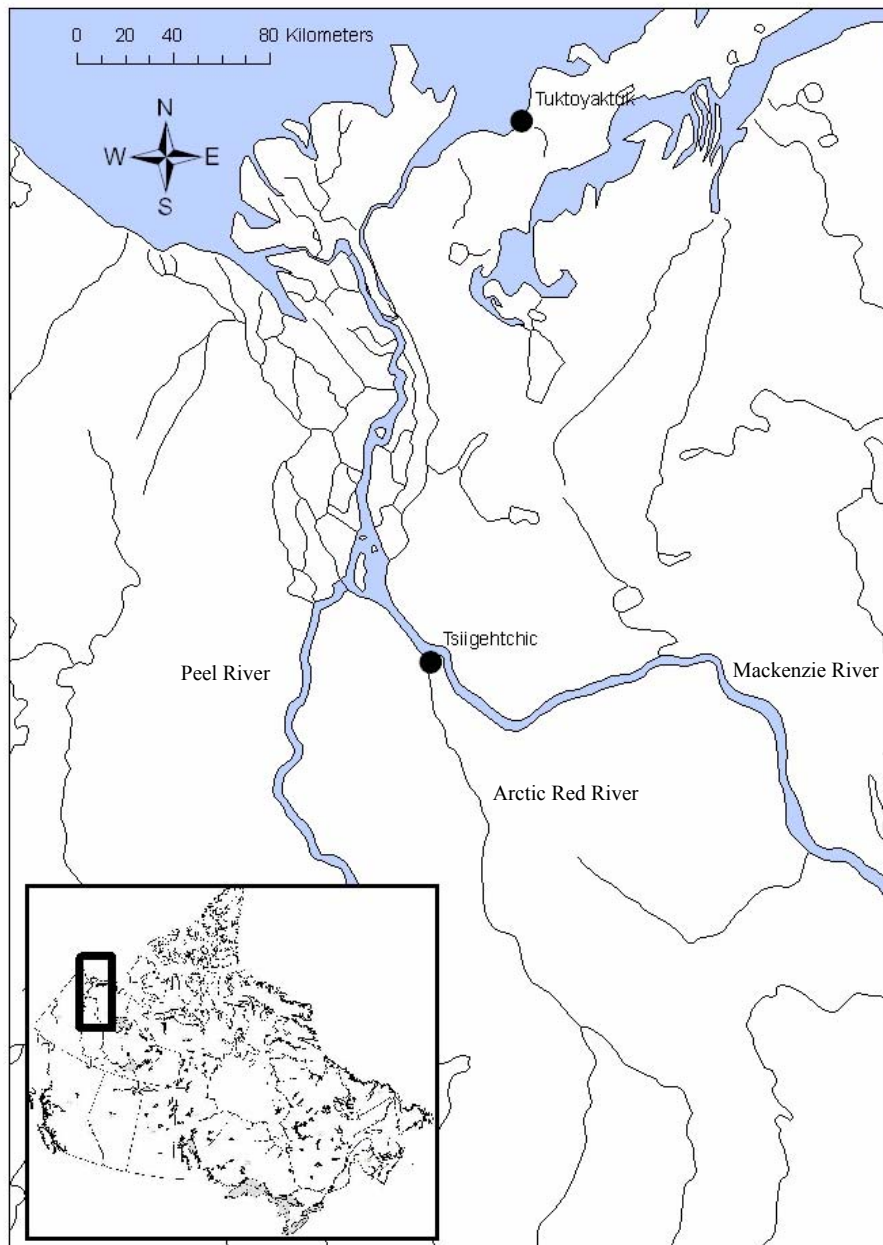


Figure 1: The lower Mackenzie River showing two of the major tributaries, The Peel River and The Arctic Red River and part of the Tuktoyaktuk Peninsula. Local community names are included as additional information and the location of the communities are represented by ●.

### *Hydrodynamics of flowing water*

The hydrodynamics of flowing water is a complex process that intrigues engineers and biologists alike. For biologists, understanding the forces that work against and with swimming fishes is important to the evolution of swimming mechanisms and behaviour (Bainbridge 1960).

There are four physical properties of water that play important roles in hydrodynamics: mass ( $M$ ), density ( $\rho$ ), viscosity ( $\mu$ ), and kinematic viscosity ( $\nu$  or  $\mu/\rho$ ) (Webb 1975). Mass is the weight of the water. Density is the amount of water molecules in a particular volume. Viscosity is the index of the fluids to resist deformation (Webb 1975). Kinematic viscosity is viscosity divided by density (Videler 1993) and is a commonly used factor in equations that determine drag on fish such as Reynolds number (Graham 1983). All four physical properties are affected by salinity, whereas temperature does not affect mass (Webb 1975). The density of water decreases with increasing temperature up to the intermittent temperature of  $4^{\circ}\text{C}$  at which point water is at its lowest density (Hynes 1972). In contrast, the viscosity of a fluid decreases continually with increasing temperature (Videler 1993).

The study of hydrodynamics theorizes fluids to be composed of fluid particles. A fluid particle is an arbitrarily defined piece of fluid that is larger than a fluid molecule, but small in comparison to the overall volume of fluid being considered (Webb 1975). The movements of fluid particles are illustrated by vector arrows. Combined vector arrows result in 'streamline' flow patterns (Webb 1975); the distance between streamlines representing water velocity. Closely spaced streamlines represent high flow regions and largely spaced streamlines represent slow water regions (Webb 1975). Stable flowing streamlines are called laminar flow, while unstable streamlines are called turbulent flow. Unstable flow occurs when there are forces acting on fluid particles in directions other than streamline (Webb 1975). In nature, laminar and turbulent flows

co-exist in flowing water and the region of change between the two flows is called the transition zone (Webb 1975).

Moving objects in a fluid (e.g. fishes swimming in a river) must overcome certain forces in order to produce forward momentum. The law of similitude describes the flow conditions around a moving object in a fluid by explaining the interactions between three main forces. These forces are inertial force, viscous force, and gravitational force (Webb 1975). A fully submerged organism has to compensate for inertial forces and viscous forces, while an organism that swims at the surface of the water has to move against inertial forces and gravitational forces (Webb 1975). Reynold's law (Blake 1983) is used to calculate the forces working against a fully submerged moving object:

$$R = \text{Inertial Force} / \text{Viscous Force}$$

### *Moving Water and Fish Migration*

Water in most environments is not static, rather it moves in a direction; this movement of water is defined as current. The speed at which the current is moving is called water velocity (Dodds 2002). Rivers are the best example of bodies of water that typically have a constant current running from the headwaters to the mouth of the river (Hynes 1972). Water velocity is a critical factor for fish that migrate (DeGraaf and Bain 1986, Jonsson 1991, Nislow *et al.* 1999, Copp and Vilizzi 2004). If the fish are travelling in the direction of the current, then the water velocity will assist fish movement. For example, if the downstream migration of juvenile Atlantic Salmon is timed with spring freshets, the juvenile fish will be partly or fully carried downstream by the flow (Northcote 1982). In contrast, anadromous adult fish on their upstream spawning migration must swim against the current. In this situation the water velocity becomes a resistant force against which the fish must swim (Webb 1975). Northcote (1982) stated that the flow and



velocity of a river has a large influence on the orientation and intensity of fish migration. Anadromous fish species and other migrating fish species like the Common Shiner (*Luxilus cornutus*) have been documented to use the flow of the river as an orientation tool by initiation of a rheotactic response directing fish to migrate upstream (McKeown 1984). In addition, it is documented that the upstream migration of many species is induced by increased river flow, as the increased flow causes a rheotactic response cuing the fish to migrate (Northcote 1982, Jonsson 1991, Trepanier *et al.* 1996, Thorstad *et al.* 1997). The reason that water velocity is a critical factor for fish migration is explained by energetics. Fish expend energy to swim. Downstream migrations which are assisted by water flow result in a reduction of energy expenditure for the fish to move from one location to another. In contrast, upstream migrations against water flow result in the fish expending more energy to move from one place to another (Quinn *et al.* 1997, Osborne 1961). In extremely high water velocity the physical flow of water can be a barrier to fish migration (Staden *et al.* 2002). Fish have a maximum swimming speed that they can achieve (Brett 1964, Webb 1975, Vidler 1993). If water velocities in a river for example, are above the maximum swimming ability of a fish this results in that section of the river being a barrier to fish passage and migration (Colavecchia *et al.* 1998). In order for anadromous fish to complete their life cycle, they must be able to swim against the current in the rivers within which they want to spawn, at the time they want to spawn.

The above information is provided as general background on the large areas of interest for this research, for example, life history theory and migration strategy, life history theory and reproductive strategy, the general area of study – the Mackenzie River Valley located in the Arctic - and the physics behind movement in water. The following section is designed to provide in depth information on the methods used in this research and the species studied (e.g. gonad development and maturation assessment, swimming performance tests, and Broad Whitefish).

### *Swimming Performance*

Most swimming performance studies have focused on southern fish populations, leaving a gap in the knowledge of Arctic freshwater fish swimming performance. Swimming performance is characterized by the relationship of swimming speed to endurance time (Wolter and Arlinghaus 2003). All swimming performance is affected by environmental factors, such as water temperature, oxygen concentration, and fish size (Hammer 1995). Swimming performance is defined by three speed categories: sustained, prolonged, and burst. Sustained swimming refers to slow swimming speeds that can be maintained for long periods of time (e.g. days, weeks, and months) (Hammer 1995). Sustained swimming is aerobic and uses red muscle fibres. The metabolic energy demand is matched by supply, and waste production is balanced by disposal (Jones 1982). Burst swimming refers to high speeds that last less than 20 seconds (Beamish 1978). It is performed anaerobically, utilizing the white muscle fibres and is terminated when intercellular energy supplies are exhausted (Jones 1982), or when waste products accumulate (Brett 1964). Prolonged swimming refers to the spectrum of swimming velocities between sustained and burst speeds (Beamish 1978) and is terminated by exhaustion. It uses both white and red muscle fibres, as well as aerobic and anaerobic processes (Peake *et al.* 2000). In this study, I assessed the prolonged swimming in Broad Whitefish under natural conditions.

Bainbridge (1963) designed the first swimming performance apparatus – the fish wheel. In the wheel, fish swam in a stationary basin, following observation marks on a rotating outer cylinder, the observation marks imitated reeds in nature and thus induced steady swimming performance (Hammer 1995). However, the fish wheel and all similar devices have limitations (Brett *et al.* 1958, Sandstrom 1983). The speed at which the wheel can turn is limited, the size (e.g. length, weight) of the test species is limited, and the fish's force of balance is affected by the

centrifugal resistance (Blake 1983). These combined factors make performance tests in a fish wheel unreliable.

More reliable approaches to studying swimming performance use a respirometer, swim tunnel, or flume. One of the first respirometers was designed by Brett (1964), to study the relationship between oxygen consumption and fish swimming speed. A swimming respirometer is a closed system, within which water circulates at a controlled velocity. The water temperature and water velocity can be altered, and dissolved oxygen may be monitored. Numerous studies over the years have utilized swimming respirometers to study fish swimming performance (Brett 1964, Jones *et al.* 1974, Thorstad *et al.* 1997, Peake *et al.* 2000).

The advantages of respirometers, the Blazka model in particular, are that they are transportable, affordable, and can be easily built (Blazka *et al.* 1960). Being transportable allows the respirometer to be taken to field research locations, rather than transporting the fish to the respirometer, thus minimizing stress. The respirometer is a closed-circuit tank, giving the researcher full control over water quality, oxygen concentration and water velocity. Closed-circuit studies permit accurate and reliable physical and chemical measures (e.g. oxygen concentration or waste production) (Cech 1990).

The disadvantage of respirometers is that fish often do not swim to physiological exhaustion when confined (Tarby 1981, Reidy *et al.* 1997, Swanson *et al.* 1998). The confinement of the apparatus and lack of water current variety (e.g. faster and slower water options) may result in an underestimation of the true swimming potential of the fish (Peake 2004). Despite these limitations, using a respirometer is the only realistic option for testing the swimming performance of Arctic fishes in their natural environment, not in a laboratory.

To assess the true swimming potential and behaviour of fish, the fish should be monitored under natural conditions. However, this can be financially and practically difficult. The closest

experimentation available that mimics nature is a flume or raceway. A flume is a long, open-ended tank that mimics the water flow of a river. Flumes may provide more accurate information on fish swimming performance and behaviour compared to other swimming performance apparatuses (Peake 2004). However, they are expensive, complex to construct, and difficult to transport.

Colavecchia *et al.* (1998) pioneered field based swimming performance tests using flumes. They used the flume to assess high speed swimming performance and swimming behaviour of migratory Atlantic Salmon (*Salmo salar*) under natural conditions by letting the fish swim voluntarily. Their findings revealed a distance-velocity barrier and corresponding low rates of passage by fish in moderate to high water velocities. Many questions arose from this study, including which method, flume or respirometer, provided more accurate data. Peake (2004) compared swimming performance results of Smallmouth Bass (*Micropterus dolomieu*) in a respirometer with results from a flume and found that mean ground speed (mean ground speed = swimming speed – water velocity) in the flume increased with water velocity, resulting in a decrease in passage time. He also found that fish successfully ascended the flume with water velocities twice the speed of the maximum determined using a respirometer, suggesting that the swimming potentials determined from respirometers underestimates the true swimming potential of the fish.

### *Fish Sexual Maturation*

Maturation is the dividing line between preparation and fulfillment in a life (Stearns 1993). The maturity of a fish is determined by the degree of gonad development. The sexing of a fish is determined by the presence of testes or ovaries (Strange 1996). The determination of maturation stage can be accomplished two ways, by visual examination of the gonads for maturity stage (e.g.

immature, mature, ripe, spent, Appendix A) or by an organosomatic index which compares the weight of a given organ to the somatic weight (Strange 1996). The organosomatic index used for maturity is the gonado-somatic index (GSI), discussed further in methods in chapters to follow.

There is a wide interspecific range for the GSI of ripe females (Wootton 1999). In species like salmonids and cyprinids, the ovaries account for 20-30% of the total body weight when females are ripe (Wootton 1979). In contrast, in some other species, primarily batch spawners, the ovaries only account for 5% of the total body weight when ripe (e.g. cichlid (*Oreochromis leucostictus*) (Wootton 1999). Batch spawners are defined as species that may spawn multiple batches within a breeding season (Kjesbu *et al.* 1996). These differences reflect the differences in the temporal pattern of egg development and spawning (Wootton 1999). Total spawners, fish that spawn once per season, typically use floodplain rivers for spawning, and will have higher GSI than batch spawners, which may spawn several times during a breeding season (Wootton 1999). Batch spawners have a low GSI at any given spawning time, but have high egg production over the entire breeding season (e.g. Threespine Stickleback (*Gasterosteus aculeatus*) and cyprinodonts (*Cyprinodon nevadensis*)) (Wootton 1999).

Testes represent a lower proportion of the total body weight compared to ovaries (Wootton 1999). For example, in a mature female stickleback, the ovaries can represent over 20% of the total body weight, while in a mature male stickleback the testes represent less than 2%. The ovaries of a mature female Atlantic Salmon can represent 20-25% of total body weight, while the testes of a male represent 3-6% of the total body weight (Wootton 1999). Overall, fish GSI can range from 2–31% in females and 0.2–16% in males (Roff 1992).

### *Broad Whitefish Biology*

Broad Whitefish (*Coregonus nasus*) is an Arctic fish species distributed widely throughout North America and north Eurasia, above the 60<sup>th</sup> parallel (Scott and Crossman 1973). Broad Whitefish are abundant in the lower Mackenzie River (downstream of Fort Good Hope) and associated tributaries and remain a subsistence food for local people (Treble and Tallman 1997). Broad Whitefish in the Mackenzie River system exhibit a complex life cycle and life history, reflecting the physical complexity of the system they inhabit (Reist and Bond 1988, Fechhelm *et al.* 1992, 1995, Reist and Chang-Kue 1997).

There are potentially three life history types of Broad Whitefish within the lower Mackenzie River (Reist 1987). Anadromous and lacustrine types have been confidently identified; it is possible that a riverine type also exists, but is yet to be properly identified (Treble and Tallman 1997, Harris and Taylor 2010). Lacustrine populations remain in freshwater for their entire life cycle (Chudobiak 1995), specifically in lakes. It is documented that lacustrine populations of Broad Whitefish reside in Travaillant Lake, NWT (Harris and Howland 2005) and Andrew Lake, NWT (Howland and Harris 2005). Like lacustrine populations, riverine populations of fish remain in freshwater for their entire life cycle, specifically rivers (Moyle and Cech 2004). Riverine populations of Broad Whitefish are speculated to reside in the Mackenzie River proper (Reist and Chang-Kue 1997); however, evidence is yet to be published. The anadromous type life history Broad Whitefish is believed to be most abundant in the Mackenzie River system (Treble and Tallman 1997, Reist and Chang-Kue 1997); and is the life history that is the focus of this study.

Several separate anadromous populations may exist, as many spawning areas have been suggested along the Mackenzie, Peel, and Arctic Red rivers (Chang-Kue and Jessop 1983, VanGerwen-Toyne *et al.* 2008, Harris and Taylor 2010). The anadromous juvenile Broad Whitefish migrate to the coast, where they occupy estuarine and semi-marine environments for

only a short period of time before entering freshwater to feed (McCart 1985). deMarch (1989) found that Broad Whitefish prefer saline concentrations of 20 parts per thousand (ppt) or below, but fish larger than 27 mm (total length) can tolerate salinities of 20 ppt or greater. Broad Whitefish appear to use coastal and saline habitats as corridors for migration between separate spawning, overwintering, and feeding areas in freshwater (Thera 1998).

Mature migrating Broad Whitefish have an average fork length of 500 mm (0.5 m) (Treble and Tallman 1997), with a range in fork length of 418 to 574 mm (Treble and Reist 1997). The average age of mature Broad Whitefish is 12 years, with a range of mature individuals from age 7 to age 30 + (Treble and Tallman 1997).

Even though Broad Whitefish migrate long distances, their body form more closely resembles that of lacustrine species (Chudobiak 1995) by being elongate, thick, and heavysset (Lindsey 1962). Broad Whitefish are laterally compressed, with their greatest body depth located anterior to the dorsal fin. The head of a Broad Whitefish is deep, wide, and short (Scott and Crossman 1973). This type of body form does not reduce the drag while swimming, indicating that Broad Whitefish must exert more energy to swim compared to a fish with a tuniform body shape (Videler 1993).

#### *Broad Whitefish Life History-Adults*

The life cycle of Broad Whitefish is complex. Broad Whitefish are an iteroparous species that may spawn every year (Howland *et al.* 2009), or every two to three years (Chang-Kue and Jessop 1983, 1991). A multi-year reproduction cycle is a common trait among northern fish populations, especially for females (Roff 1992). Short growing seasons and highly variable climates may slow or inhibit yearly gamete production (Thera 1998) forcing individual fish to skip one to two years between spawning runs (Reist and Chang-Kue 1997). Each year, the Broad

Whitefish population is divided into two groups: spawners and non-spawners (Thera 1998). The proportion of individuals within each group varies from year to year and is dependent on seasonal productivity of the environment for that year and previous years.

Sexually mature Broad Whitefish begin migrating in July and August from freshwater systems on Richard's Island and the Tuktoyatuk Peninsula (Lawrence *et al.* 1984), into the central delta where they wait in holding pools (Reist and Chang-Kue 1997, Chang-Kue and Jessop 1983). In September or October the fish continue migration upstream from the central delta to the spawning sites (Chang-Kue and Jessop 1983, Howland *et al.* 2009). Four distinct spawning areas have been proposed: 1) upstream of the Arctic Red River; 2) Point Separation, on the main stream of the Mackenzie River; 3) upper reaches of the Peel River, and 4) the Ramparts Rapids on the Mackenzie River, near the town of Fort Good Hope (Chang-Kue and Jessop 1983, Howland *et al.* 2009). There are numerous published studies on the movement of Broad Whitefish within the Mackenzie River system, referencing the Arctic Red River as being important for spawning (Chang-Kue and Jessop 1983, 1991, and 1992, Reist and Bond 1988, Chudobiak 1995, Reist and Chang-Kue 1997, Thera 1998, Tallman *et al.* 2002, Howland *et al.* 2009). Presently there is no published literature on the spawning condition of Broad Whitefish migrating in the Arctic Red River. It is one of the objectives of this research to assess the sexual maturity of migrating Broad Whitefish in the Arctic Red River.

Broad Whitefish that are resting (not spawning) in a given year migrate with the spawning population to the inner delta, where deep eddies can be used for pre-spawning aggregations (Stein *et al.* 1973, Chang-Kue and Jessop 1983). From the inner delta, some of the non-spawners are suspected to migrate with the spawning population further upstream (Thera 1998), while others either remain in the inner delta or return to the coast for overwintering.



The most important tributary to the current study is the Arctic Red River, which provides important spawning grounds for Broad Whitefish (Reist and Bond 1988, Bodaly *et al.* 1989, Bond and Erickson 1992). The timing presence (catch-per-unit-effort (CPUE)), categorized maturity (e.g. Female immature, mature, ripe, spent, resting; Male immature, mature, ripe, spent, resting (Appendix A)) and measured maturity (GSI) of migrating Broad Whitefish in the Arctic Red River have yet to be published. Broad Whitefish are speculated to spawn under the ice during late October and early November, when water temperatures are near 0°C (Chang-Kue and Jessop 1992).

#### *Broad Whitefish Life History - Young-Of-The-Year*

The fertilized eggs of Broad Whitefish develop over the winter months and hatch in early spring (April and May) (Reist and Chang-Kue, 1997). The flow rate of the river determines the intensity and date of hatching, as Broad Whitefish embryos are sensitive to mechanical perturbations (Bogdanov *et al.* 1991). The high flow rate of the river during spring break-up physically stimulates the embryos to initiate hatching (Bogdanov *et al.* 1991).

There is a temporal hatching gradient that is linked to spring break-up. Larvae at spawning sites around Fort Good Hope will hatch sooner than larvae at spawning sites further north (downstream), like the Arctic Red River, or Point Separation (Thera 1998). The fry emerge from the gravel and are swept downstream under the ice during spring flooding (Reist and Chang-Kue 1997). The majority of the fry are swept downstream through the delta, some are swept eastward along the Tuktoyaktuk Peninsula, and still others are carried out into the western channels of the delta and then eastward into the outer delta near Richard's Island (Reist and Chang-Kue 1997).

In late June to mid-July, the young-of-the-year (YOY) migrate from the Tuktoyaktuk Peninsula and Richard's Island up newly-opened freshwater creeks, into large, warm water, highly

productive tundra lakes (Bond 1982, Chang-Kue and Jessop 1992). These lakes are a productive feeding ground and safe overwintering area for yoy and other juvenile fish within the lake (Reist and Chang-Kue 1997).

The timing of spring break-up, flow, volume and discharge are critical factors that influence the abundance and composition of fish populations in the Mackenzie Delta during the summer. These factors also indirectly affect the survival rate and year class strength of yoy and juvenile Broad Whitefish (Reist and Chang-Kue 1997). To ensure that embryos are fully developed by the time of spring flooding, it is imperative that adult Broad Whitefish spawn at the appropriate place during the appropriate 'time-window' during the previous fall.

#### *Broad Whitefish Life History - Juvenile*

Immature Broad Whitefish (length < 300 mm) disperse throughout the Mackenzie Delta in tundra lakes (Thera 1998), where they remain until the age of four years (length 300 – 450 mm). They then begin complex spring migrations from the freshwater lakes into coastal waters for the purpose of feeding (Chang-Kue and Jessop 1992). Some older juveniles (length 300 – 450 mm) overwinter in the coastal waters of the outer delta and nearshore bays. Other older juveniles return in the fall to the freshwater tundra lakes to overwinter (Chang-Kue and Jessop 1992).

Sexual maturation in Broad Whitefish begins at seven or eight years (Bond 1982, Chang-Kue and Jessop 1992). Mature individuals begin migrating to the delta in July, where they mix with the existing adult population (Bond and Erickson 1985, Chang-Kue and Jessop 1992).

#### *Broad Whitefish Swimming Form - Subcarangiform*

Broad Whitefish are classified as subcarangiform swimmers. Subcarangiform swimming mode is defined by a fish having more than one half wave but less than one full wave present on

the body at any given time (Lauder and Tytell 2006). Subcarangiforms have a propulsive wave that is small (lower amplitude) at the snout, and decreases along the body axis to a minimum amplitude being at the posterior end of the operculum (Bainbridge 1963). As the wave travels from the operculum towards the posterior end of the tail it increases in amplitude to maximum amplitude at the tip of the tail (Bainbridge 1963, Webb 1975). The caudal fin of subcarangiform swimmers is extremely flexible and has a complex motion separate from the propulsive body wave (Webb 1975). The maximum amplitude of a tail beat in a swimming fish is approximately 0.2 times the body length (Bainbridge 1958). This is important to consider when testing fish swimming speed in a confined space (e.g. swim tunnel), as contact with the sides of the tank can affect swimming potential and may need to be corrected for. Undulatory swimming speed is controlled by changes in tailbeat frequency among all species and swimming modes. Faster wave propulsions along the body, caused by faster contractions of the lateral muscles results in faster swim speeds (Shadwick and Gemballa 2006).

## *Objectives*

The purpose of this research was to increase knowledge of the spatial and temporal use of the aquatic habitat by Broad Whitefish during their spawning migration in the Arctic Red River, NWT. It should be noted that habitat in this research refers to the habitat of the water column in a river with reference to the spatial distribution within the river (distance from bottom, distance from side) and to the habitat selected based on water velocity.

The first step in this research was to confirm that sexually mature Broad Whitefish were migrating up the Arctic Red River to spawn. I hypothesized that Broad Whitefish have a defined migration time up the Arctic Red River and that the reason for the migration is for spawning. To assess the presence and timing of migration, changes in CPUE were used. It was expected that CPUE would be highest when fish were migrating and lowest before and after migration. To assess spawning condition of the fish visual assessment of the gonadal development as well as measures of gonad weight to body weight were used to determine maturity stage. It is expected that fish preparing to spawn have gonads that are visually mature and are heavier due to increased egg and milt production.

From there, I used a cumulative logit model to look at what factors influence maturity stage development during migration and the characteristics of Broad Whitefish migration. I hypothesized that gonad weight (GSI), timing (date) and abundance (CPUE) could be used to predict maturity stage of migrating Broad Whitefish. I expected that gonad weight was important in predicting maturity stage because mature gonads are large masses that weight more compared to immature or resting gonads. Timing (date) was expected to be important since it is a critical factor to successful spawning and subsequent larval emergence. Lastly, abundance of fish was expected to be important as most fish spawn in large congregations.

Once it was confirmed that the Broad Whitefish were using the Arctic Red River to spawn, I assessed if they exhibited any habitat selection by examining the preferred water velocity during migration. This was done by identifying the location within the water column where the fish were caught, and correlating it to water current profiles. It was expected that Broad Whitefish would swim in the lowest flowing water velocities because this is a typical energy conservation technique exhibited by other migrating fish species.

Lastly, I used a swim tunnel to develop a swim curve of Broad Whitefish prolonged swimming to compare with water velocities naturally selected during migration. Swimming performance tests were used to determine the swimming ability of Broad Whitefish. These results were compared to water velocities found in the natural environment to assess if any areas of the river were barriers to fish migration. I hypothesized that Broad Whitefish would be able to swim at water velocities higher than most of the water velocities present in the Arctic Red River at the time of migration, but that some water velocities may be limiting to Broad Whitefish migration as this is commonly noted in other migrating anadromous fish species (Quinn 2005, Thorstad *et al.* 2008).

## **Chapter 2: Identifying the migration timing and type of a Canadian Arctic fish-Broad Whitefish (*Coregonus nasus* (Pallas 1776)).**

### **INTRODUCTION**

Migration is a common trait among Arctic fish species which allows access to physically separate critical habitats such as overwintering areas (Northcote 1978) and spawning habitats (Brannon 1981). Migration is defined as the movement from one vital habitat to another vital habitat (Roff 1992). Dingle (1985) proposes that migration evolves in response to the variable nature of the habitats in which larvae and/or adults reside.

The Arctic is characterized by: extreme seasonal climate and weather (Wrona *et al.* 2005), low or absent sunlight in winter, long days during the summer (McBean 2005) and prevalence of seasonal ice and snow cover (Wrona *et al.* 2005). Despite the extreme and difficult conditions of the Arctic many fish have evolved to thrive in the Arctic; they are classified under the Arctic Fish Guild (Reist 1994).

Arctic fish, as with most fish species, have predictable routes of migration and predictable timing (e.g. seasonally) that correlate with certain life stages (Brannon 1981, Roff 1992). The predictable spatio-temporal migration is theorized to place individuals in the most optimal habitat at the most optimal time (Brannon 1981, Miller and Brannon 1981). Within the Arctic environments the timing of migration becomes critical as certain habitats (e.g. spawning grounds) are open for only short seasonal periods (e.g. summer and fall).

Anadromy is the predominant migration pattern among Arctic fish species (Gross *et al.* 1988). Anadromous fish divide their life cycle between freshwater and saltwater, experiencing most of their growth in saltwater while returning to freshwater for reproduction and spawning (Moyle and Cech 2004, McDowall 1997). Anadromous spawning migrations are physically demanding and therefore energetically expensive. Spawning sites are typically upstream of

feeding sites (Brannon 1981, Miller and Brannon 1981, Northcote 1982, Reist and Chang-Kue 1997, Howland *et al.* 2000); enabling downstream migration of larvae and juveniles but increasing the cost of upstream migration of mature adults. Migrations of anadromous Arctic fish species can be short for example, some Atlantic Salmon populations migrate only 24 km upstream to spawning sites (Dutil 1986), or extensive for example, some Inconnu (*Stenodus leucichthys nelma*) populations migrate up to 1500 km upstream to spawning sites (Howland 1997, Alt 1977). The length of the migration of individual fish populations depends on the life history of the species and populations in question.

There has been extensive research on the migration routes, patterns and timing of many southern species, such as Pacific salmon (Miller and Brannon 1981, Keefer *et al.* 2004, Quinn 2005, Saiget *et al.* 2007), Atlantic Salmon (Martin *et al.* 2009, Plantalech Manel-La *et al.* 2009, Siira *et al.* 2009), American Shad (Leggett and Carscadden 1978, Olney *et al.* 2006, Hoffman *et al.* 2008), lamprey species (Beamish 1979, Andrade *et al.* 2007, Adams *et al.* 2008, Keefer *et al.* 2009) and eel species (Aarestrup *et al.* 2008, Acou *et al.* 2008, Overton and Rulifson 2009). In contrast little work has been done on the migration of Arctic fish such as, Inconnu (Alt 1977, Howland 1997, Howland *et al.* 2000, 2001, Stephenson *et al.* 2005), Broad Whitefish (Hatfield *et al.* 1972, Stein *et al.* 1973, Bond and Erickson 1985, Chang-Kue and Jessop 1991, Reist and Chang-Kue 1997, Tallman *et al.* 2002), Lake Whitefish (Lambert and Dodson 1990) and cisco species (*Coregonus sardinella* and *Coregonus autumnalis*) (Kline *et al.* 1998). The most extensive migration study of Canadian Arctic fishes was undertaken by Chang-Kue and Jessop (1991) in the Mackenzie River Valley, in response to potential oil and gas development in the Arctic. Chang-Kue and Jessop (1991) performed a tagging study that provided information on the migration of coregonids (member of the Coregonidae family) from overwintering areas along the Tuktoyaktuk coast to potential spawning grounds upstream. From the study by Chang-Kue and Jessop (1991)

and other studies by Jessop *et al.* (1974), VanGerwen-Toyne *et al.* (2008), and Howland *et al.* (2009), two major tributaries of the Mackenzie River have been identified as potentially important for spawning migrations: the Peel River and the Arctic Red River. The migrating population of coregonids in the Peel River was intensively monitored by VanGerwen-Toyne *et al.* (2008). It was determined that Inconnu, Arctic Cisco, Broad Whitefish, Lake Whitefish and Least Cisco preparing to spawn, migrated up the Peel River, hence indicating this river's importance for coregonid spawning. VanGerwen-Toyne *et al.* (2008) were able to provide baseline information on the timing of migration for different coregonids along with biological information on the population structure (e.g. age, fecundity, fork length). In contrast to the Peel River study there has been little work looking at the importance of the Arctic Red River, an alternative spawning tributary (Chang-Kue and Jessop 1991).

The purpose of my study is to fill in gaps on the migration of Broad Whitefish in the Arctic Red River, a tributary of the Mackenzie River (Figure 1). In my study was able to identify critical migration timing by use of catch-per-unit-effort (CPUE) as an index of abundance. As well I was able to determine if the migrations are for spawning by looking at the maturity stage and gonadosomatic index (GSI) of the fish captured. Finally, I present a cumulative logit model that utilizes GSI, CPUE and timing (date) data to determine the probability of maturity stage of migrating fish to investigate the characteristics of Broad Whitefish migration in the Arctic Red River.



## MATERIALS AND METHODS

### *Study Site*

The Arctic Red River is the study site for this research. Along the Arctic Red River in 1992 and 1993 there were multiple locations where nets were set (Figure 2), from the mouth of the river and upstream. The field season ran from September to November in 1992 and July to November in 1993; this research was part of a study undertaken by Fisheries and Oceans Canada (DFO). The Arctic Red River was selected as the study site because Traditional Knowledge of local Gwich'in people state that Broad Whitefish spawn in the upper reaches of the Arctic Red River (Greenland and Walker-Larson 2001) and tagging studies by Change-Kue and Jessop (1991) and Howland *et al.* (2009) show that Broad Whitefish migrate up the Arctic Red River at the proposed time of spawning.

### *Fish Capture Methods*

In 1992 and 1993 fish were caught using 12.7 cm (5.0 inch) stretched-mesh gill nets, as well as experimental gill nets with panels of 3.8 cm (1.5 inch) to 10.1 cm (4 inch) stretched-mesh size (Chudobiak 1995, Tallman *et al.* 2002). Gill nets were set perpendicular to the shore in eddies and left to soak for 24 hours a day, except during freeze-up (Chudiobiak 1995, Howland 1997, Tallman *et al.* 2002). After ice freeze-up, nets were set under the ice using the willow branch method (Hubert 1996); this technique is similar to the traditional Gwich'in method used to set nets under the ice. Net sets were typically 24 hours; in rare instances (e.g. high levels of debris in the river, ice development over the net, difficulty getting to nets due to ice formation) the net set may have been shorter or longer. Fish were removed from the gill nets and biologically sampled for fork length (the length from the snout to the fork in the tail, mm), round weight (the whole weight

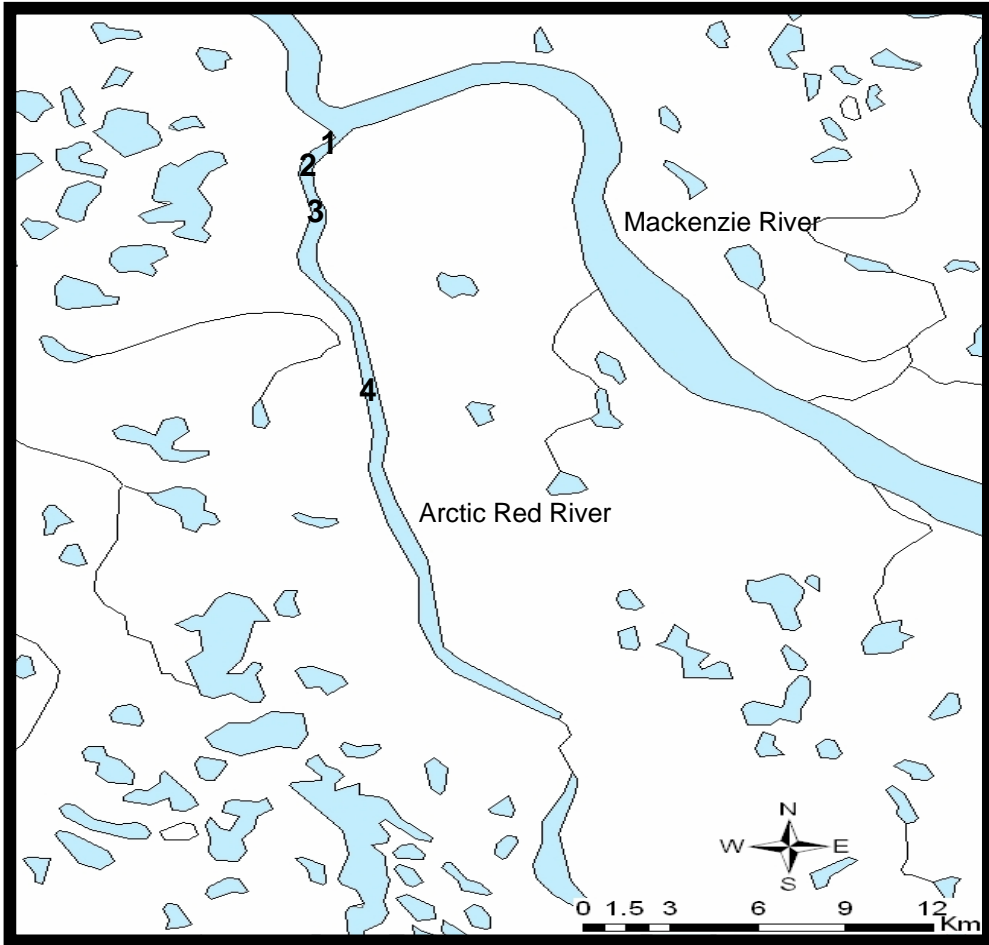


Figure 2: Map of the gill netting stations on the Arctic Red River for 1992 and 1993 data collection. 1: Station 113, Station 114; 2: Station 112, Station 118, Station 119; 3: Station 111, Station 115, Station 104, Station 110, Station 108; 4: Station 122 (Seven Miles).

of the fish, kg), sex, maturity stage, gonad weight and aging structure (otoliths). Ovaries from mature female Broad Whitefish were collected in 1992 and 1993 and frozen (Chudobiak 1995, Tallman *et al.* 2002).

#### *Timing of Migration - Catch-Per-Unit-Effort(CPUE) Analysis*

To quantify seasonal changes in relative abundance of Broad Whitefish, catch-per-unit-effort (CPUE) was calculated, with effort standardized to a 23 X 1.8 m net (Howland 1997). CPUE was calculated for each set by dividing the standardized catch for that set by soak time (in hours) (Howland 1997). To better demonstrate the trend of CPUE a piecewise regression was fitted to the data and used to show the change in slope of CPUE. Piecewise regression provides a better visual and statistical reference for trend lines in data with changing slopes (Crawley 2007, Toms and Lesperance 2003). The piecewise regression was fitted at numerous break points (model 2 = 1 break point, model 3 = 2 break points, model 4 = 3 break points) and Akaike's Information Criterion (AIC) (Anderson 2008) was conducted to determine which piecewise regression line best fit the data. In addition to the piecewise regression, non-parametric smooth curves (loess, gam and polynomial regression) were fitted to the CPUE data to analyze the change in slope. The loess is a locally weighted procedure for fitting a regression line to data through multivariate smoothing (Cleveland and Devlin 1988). The final loess smooth represents the relationship between the dependent and independent variables (Quinn and Keough 2002). The loess is created by calculating the ordinary least squares (OLS) and smoothing the dependent variable as a function of the independent variable (Cleveland and Devlin 1988). The dependent variable is calculated differently for each independent variable depending on how far the dependent variable is from the target x-value using a tri-cube weight function (Quinn and Keough 2002). The gam curve uses a generalized additive model (hence the name gam) to create the non-parametric

smooth curve (Bolker 2008) by building on the loess smoothing function (Quinn and Keough 2006). The additive term in the name gam refers to the response variable being modeled as the sum of functions of each predictor without interactions. The gam smoothing function for each predictor is derived from the data independently from the smoothing function of any other predictor (Quinn and Keough 2006). The polynomial modelling tool uses a linear model with a polynomial function to create the smooth line ( $x^x$ ) (Crawley 2007). For further information and R coding on piecewise regression, AIC and non-parametric smooth curve modelling, refer to Appendix D, Appendix E and Appendix F, respectively.

#### *Purpose of Migration – Maturity Stage and Gonadosomatic Index Analysis*

Sex for each Broad Whitefish (n = 1063, both 1992 and 1993) was determined by the presence or absence of eggs in ovaries and milt in testes (Chudobiak 1995). A qualitative description of the degree of gonad development was determined using the Bond and Erickson (1985) scale (Appendix A). The following were the maturity categories used for each sex: Immature, Mature, Ripe, Spent and Resting. The subjective gross examination of the gonads is often used, but can lead to unreliable information on maturity stage in whitefish (Bond 1982). The assessment is subjective and often maturity stages of whitefish do not appear drastically different from one stage to the next, making visual maturity assessment unreliable at times (Bond and Erickson 1985). A more objective assessment of maturity stage is achieved by using the gonadosomatic index (GSI) (Bond and Erickson 1985). The formula used to estimate gonadosomatic index was:

$$\text{GSI} = \text{gonad weight} / (\text{body weight} - \text{gonad weight}) \times 100 \text{ (Howland 1997, Roff 1992)}$$

### *Correlation between timing and purpose of migration*

A generalized linear model (GLM) was used to statistically analyze the correlations between fish maturation (GSI and Maturity Stage), abundance (CPUE) and date. GLM uses maximum likelihood (ML) to fit the model to the data, with the following 3 components: random component, systematic component and a link function, which links the random and systematic components (Quinn and Keough 2006). Specifically I looked at the 2 following general equations over different time scales of the 1993 field season, females and males were treated individually:

$$\text{GSI} \sim \text{Cpue} + \text{Date}$$

$$\text{Maturity Stage} \sim \text{Cpue} + \text{Date}$$

Time scales were: the entire field season (all data), July to September, September to mid-October, mid-October to mid-November, before Oct 30<sup>th</sup> and after October 30<sup>th</sup>. A quasi-binomial GLM with a logit link function was selected to allow the model to estimate the dispersion of the parameters from the data. The GLM was modeled in R and output for each GLM and R coding can be found in Appendix L.

### *Migration Characteristics - Logit Model Analysis*

A cumulative logit model was used to model the effects that predictor variables (GSI, CPUE and date) have on the categorical response variable (maturity stage). The basic model for a  $c$ -category ordinal response variable  $Y$  and a set of predictors  $x$  with corresponding effect parameters  $\beta$  is:

$$\text{logit} [ P (Y \leq_j | x) ] = \alpha_j - \beta x, j = 1, \dots, c-1$$

Where  $Y$  = the categorical response variable, maturity stage;  $x$  = the predictor variable(s), GSI, CPUE and date;  $\alpha_j$  = the cut points between each maturity stage category;  $\beta x$  = the effect parameters of corresponding  $x$  (slope of the line). The parameter  $\alpha_j$ , called ‘cut points’ is used to separate the  $Y$  variable into categories (Lui and Agresti 2005). Model fitting was accomplished by maximum likelihood (ML) and the model was executed using SAS 9.1, using the link=glogit option (Stokes *et al.* 2009). Due to the range in GSI values, I separated females from males for each individual year (1992 and 1993) and ran the model on each year and each sex. For more information on the model and coding used in SAS see Appendix G and Appendix H, respectively.

## RESULTS

### *Timing of Migration - Catch-Per-Unit-Effort (CPUE)*

Although the abundance of Broad Whitefish differed between years (1993 having a higher abundance than 1992), the timing of Broad Whitefish migration through the Arctic Red River was similar in both years (Figure 3 and Figure 4). Broad Whitefish were in low abundance in the Arctic Red River during the summer months (beginning of July to the end of August) (Figure 3, Figure 4). Abundance increased in the Arctic Red River over September with a distinct peak between late October and very early November (Figure 3, Figure 4). Abundance of Broad Whitefish drastically declined in the Arctic Red River starting around the 3<sup>rd</sup> to 5<sup>th</sup> of November (1992 and 1993, respectively) (Figure 2, Figure 3), suggesting that Broad Whitefish had moved out of the sampling area in the Arctic Red River. Gillnetting under the ice continued until mid-November with marked decreases or absence of Broad Whitefish in the catches (Figure 3, Figure 4).

The slopes determined from the piecewise regression show this change in trend (Table 2). For 1992 data, the model 4 piecewise regression (Figure 5) was selected using the AIC method. This model had the lowest AIC value (120.6621) compared to the AIC values for model 2 (135.9041) and model 3 (128.0116) from the piecewise regression analysis. It is commonly accepted that when models have AIC values with a difference of 4 or more, the models are distinguishable different (Bolker 2008). For 1993 data, the model 4 piecewise regression (Figure 6) was selected using the AIC method, model 4 had the lowest AIC value (636.6315) compared to model 2 (783.3800) and model 3 (643.5467).

The non-parametric smooth curves for 1992 and 1993 data (Figure 7 and Figure 8) support the trend that the piecewise regression shows - an increase in CPUE over the course of the summer and into the fall, followed by a drastic decrease in November. Visually it appears that the loess

smooth curve seems to provide the best fit for both years of data compared to the gam and polynomial smooth curves (Figure 7 and Figure 8).



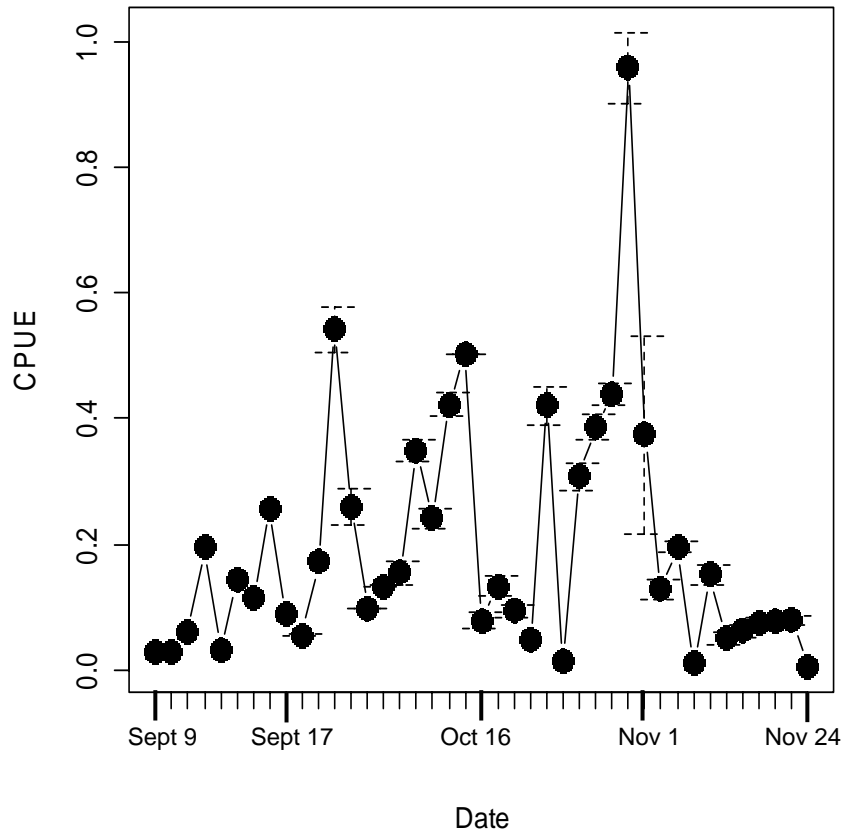


Figure 3: Plot of the Means for 1992 CPUE, standardized for net length and net depth, both experimental and commercial nets included, n = 626. Standard error bars included.

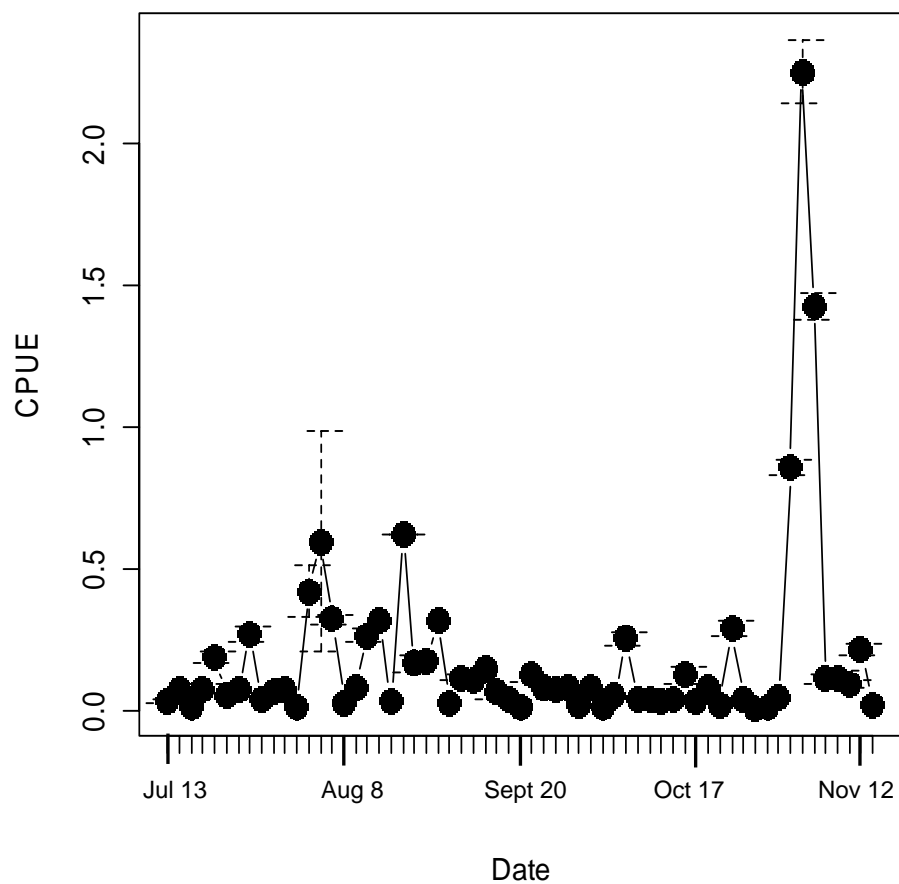


Figure 4: Plot of the Means for 1993 CPUE, standardized for net length and net depth, both experimental and commercial nets included,  $n = 437$ . Standard error bars included.

Table 2: Piecewise regression results from the 1992 and 1993 CPUE data. The slopes and intercepts of each line and corresponding dates are provided.

<b>Year</b>	<b>Date</b>	<b>Slope</b>	<b>Intercept</b>
1992	September 10 to October 13	0.000101	0.25071
1992	October 14 to October 17	-0.083014	24.38698
1992	October 18 to October 31	0.020703	5.826533
1992	November 1 to November 25	-0.038252	12.366959
1993	July 13 to August 25	0.006365	1.133177
1993	August 26 to October 25	0.011417	-2.887276
1993	October 26 to November 5	-0.311086	95.165789
1993	November 6 to November 15	-0.001301	0.615430

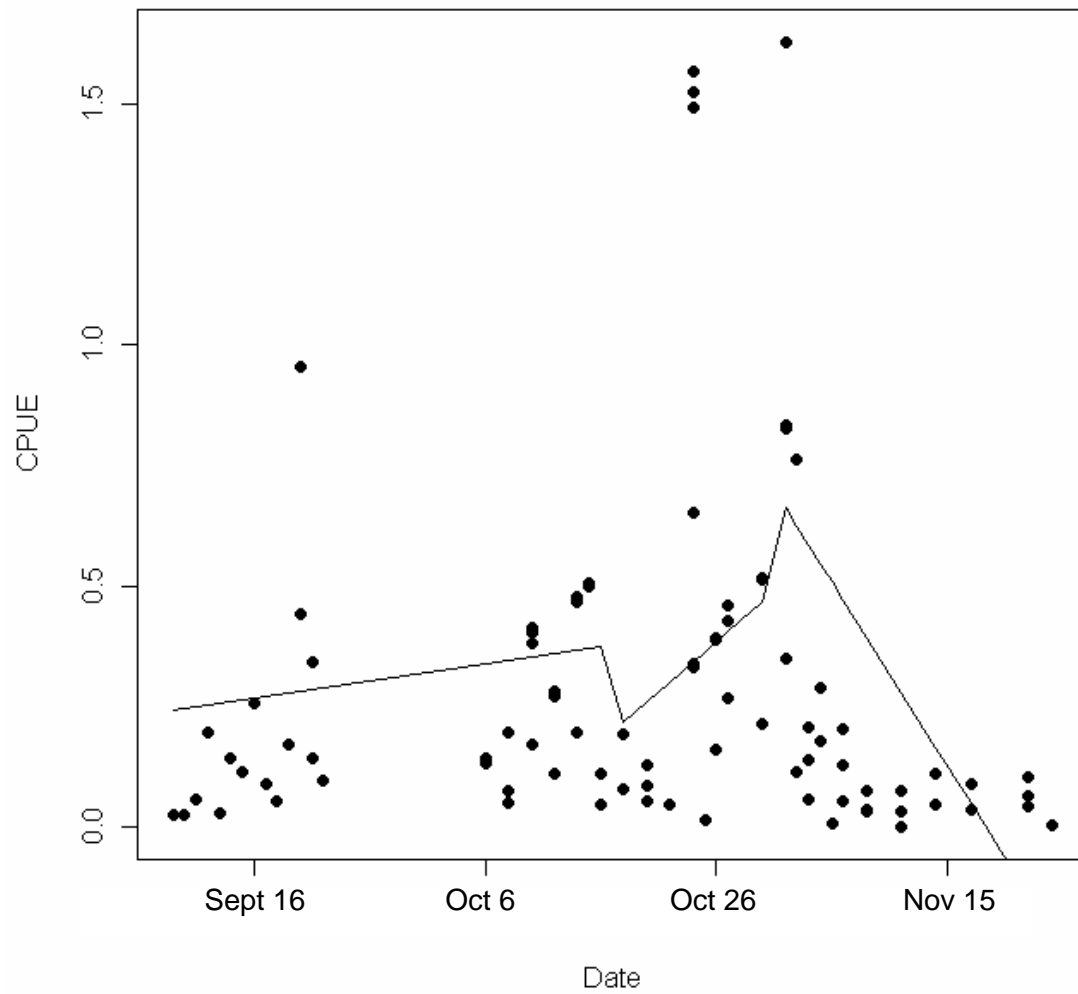


Figure 5: Piecewise regression fitted to 1992 CPUE data, using AIC to select modeling line. Table 2 reports the slopes and intercepts for the different lines determined by the piecewise regression.

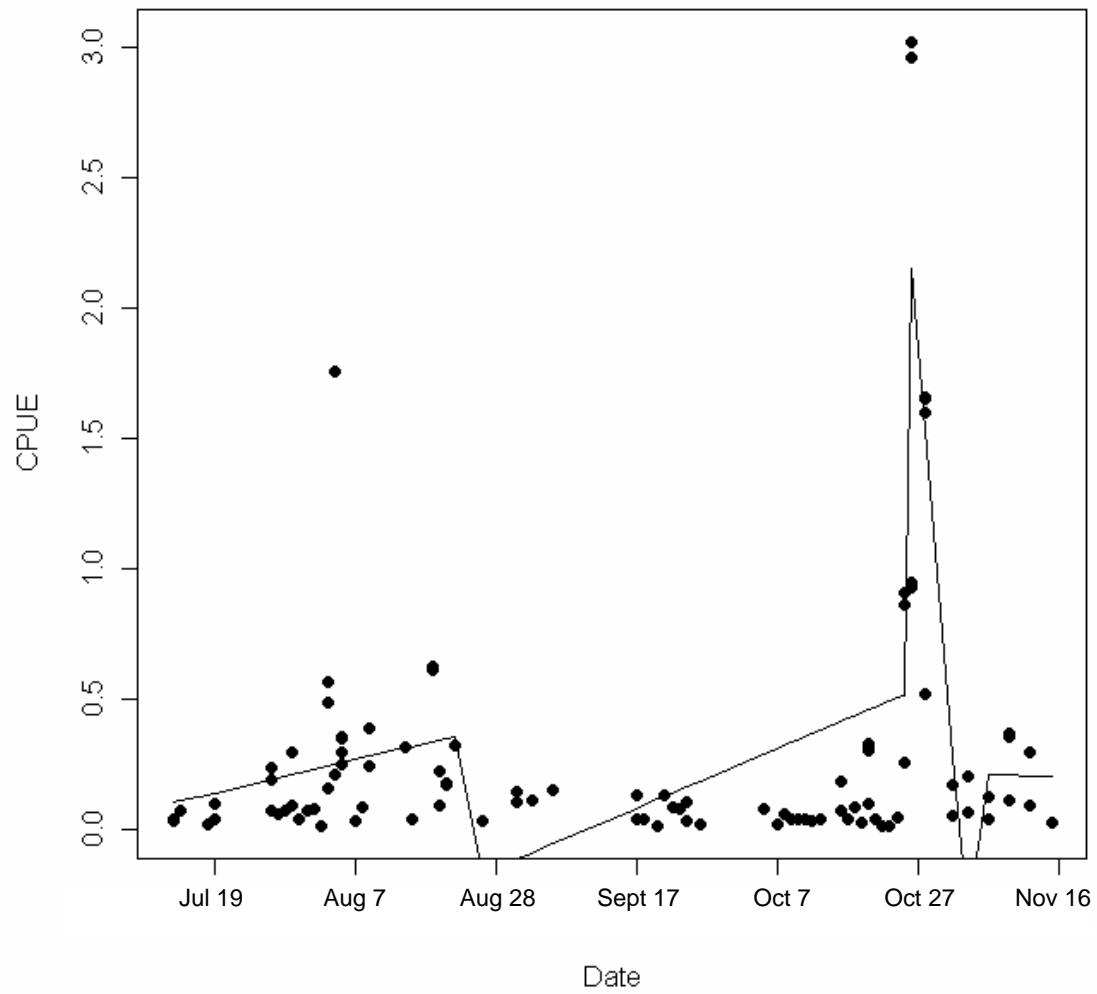


Figure 6: Piecewise regression fitted to 1993 CPUE data, using AIC to select modeling line. Table 2 reports the slopes and intercepts for the different lines determined by the piecewise regression.

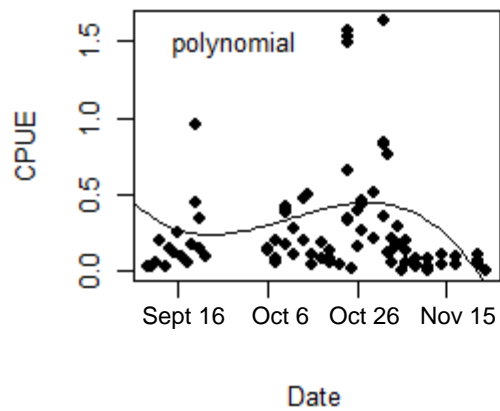
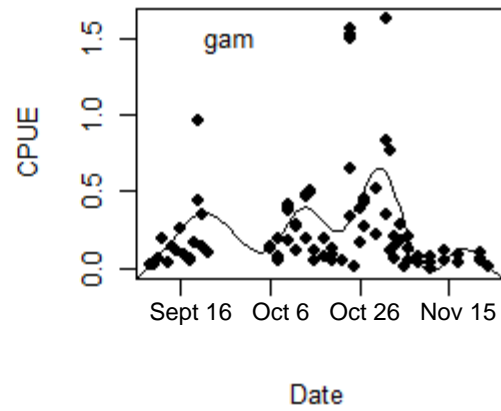
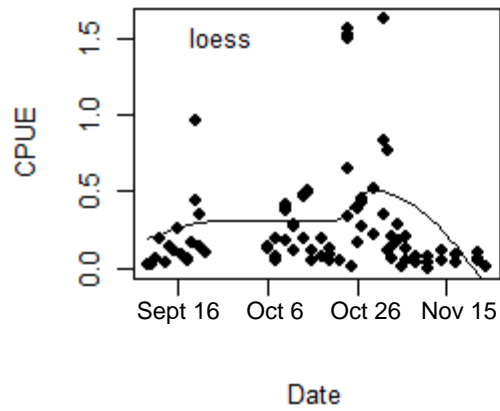


Figure 7: Non-parametric smooth curves (loess, gam and polynomial) plotted with Broad Whitefish CPUE data from the Arctic Red River (1992). The name of the smooth curve modelled is in the top left-hand corner of the each graph.

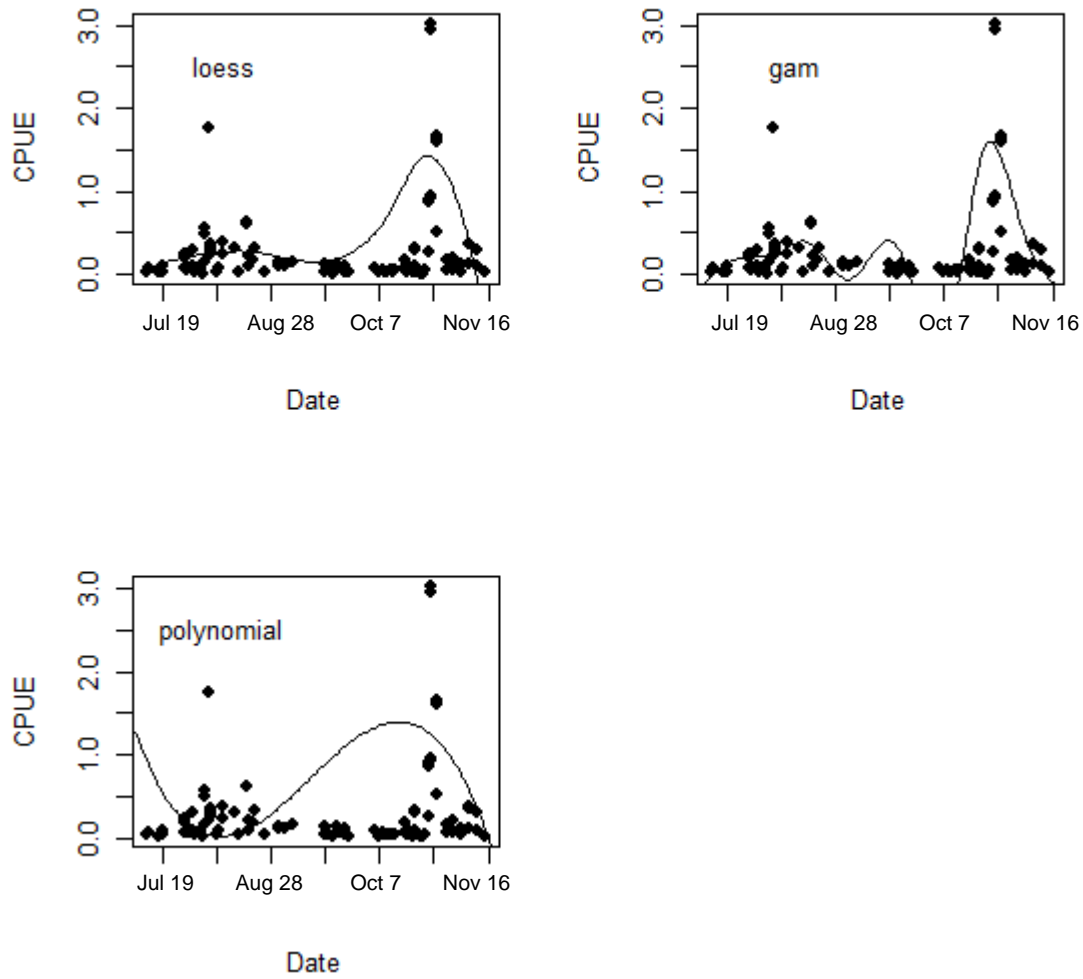


Figure 8: Non-parametric smooth curves (loess, gam and polynomial) plotted with Broad Whitefish CPUE data from the Arctic Red River (1993). The name of the smooth curve modelled is in the top left-hand corner of the each graph.

### *Purpose of Migration - Maturity Stage and Gonadosomatic Index*

For the maturity stage analysis only the data from 1993 was used, as the 1992 data was insufficient and inconsistent for a number of reasons. According to Kimberly Howland (personal communication, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba) many changes in personnel occurred during the first three months of the study in 1992 and most of the Broad Whitefish captured in 1992 were floy tagged and released, which respectively are likely the causes of the inconsistent and the insufficient classification of 1992 maturity (Appendix I). In 1993 females were categorized as: mature, ripe, spent or resting; and the males were categorized as: immature, mature, ripe, spent or resting, (Table 3). The maturity stage analysis indicates that sexually mature female Broad Whitefish first appeared in the gill nets in late July and ripe female Broad Whitefish first appeared in the gill nets in small numbers in mid-September (Figure 9). Similar to females, mature male Broad Whitefish first appeared in gill nets in early August and ripe males first appeared in gill nets in mid-September (Figure 10). Unlike the females, there were a large number of ripe males caught in late October, in particular on October 27<sup>th</sup>, 1993. Post-spawners (maturity stage spent) of both female and male Broad Whitefish first appeared in the gill nets after October 29<sup>th</sup>, 1993 (Figure 9, Figure 10). After the first week in November, most captured Broad Whitefish were spent adults, assumed to be migrating downstream towards overwintering grounds (Figure 9, Figure 10).

For the quantitative maturity analysis using GSI both 1992 and 1993 data was used. There was an increase in the relative GSI of female Broad Whitefish from the end of August to the end of October, with the highest GSI recorded between October 15<sup>th</sup> and October 26<sup>th</sup> (Figure 11). The rise in GSI coincided with the marked increase in abundance of Broad Whitefish in the Arctic Red River, indicating that these fish were in spawning condition. Following the rise of GSI in mid to late October, there was a drastic decrease in the GSI (from 25 to <10) of captured females. Female



Broad Whitefish GSI ranged from 5 to 35 over the different maturity stages (Figure 11); in contrast, male Broad Whitefish GSI ranges from 0.5 to 2.5 over the different maturity stages (Figure 12). There was a slight increase in the GSI of male Broad Whitefish captured in the Arctic Red River between early September and early November. This increase was followed by a decrease in GSI from approximately 2.0 to approximately 0.5. Males classified as ripe had GSI ranging from 1.5 to 2.5 (Figure 12).

A visual assessment of the maturity stages of the fish corroborated that elevated GSI corresponds to further developed gonads in both female and male Broad Whitefish (Figure 13, Figure 14). When female GSI was calculated at 0.17 or higher the maturity stage corresponded to ripe, when GSI was calculated between 0.6 and 0.17 the maturity stage was assessed as mature, and the lowest female GSI corresponded to a maturity of spent (Figure 13). Like female Broad Whitefish, male Broad Whitefish with elevated GSI levels are classified at higher maturity stages. The GSI of male Broad Whitefish does not drastically change between maturity stages; however, mature and ripe males on average have the highest GSI (Figure 14).

Table 3: Maturity stage classification of Broad Whitefish in the Arctic Red River for 1993 and the number of individual fish caught and classified at each maturity stage.

*Females*

<b>Year</b>	<b>Maturity Stage</b>	<b>Sample size (n)</b>
1993	Mature	27
1993	Ripe	15
1993	Spent	10
1993	Resting	5

*Males*

<b>Year</b>	<b>Maturity Stage</b>	<b>Sample size (n)</b>
1993	Immature	3
1993	Mature	10
1993	Ripe	84
1993	Spent	42
1993	Resting	6

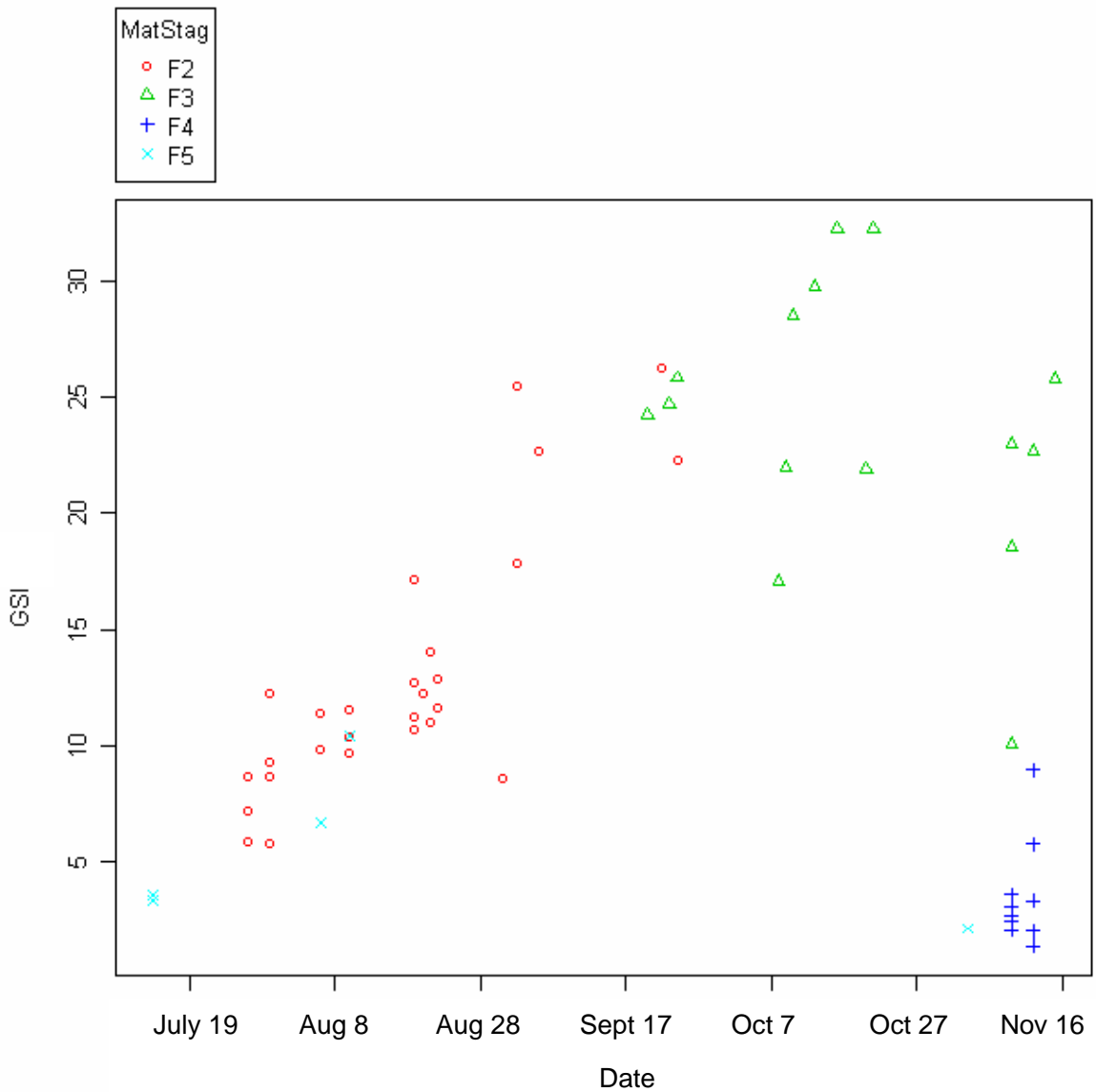


Figure 9: Graph of the GSI by date of female Broad Whitefish captured in the Arctic Red River in 1993. The individual fish are categorized by maturity stage from the visual observation in the field. Mature females (F2) = O; ripe females (F3) = Δ; spent females (F4) = +; and resting females = x.

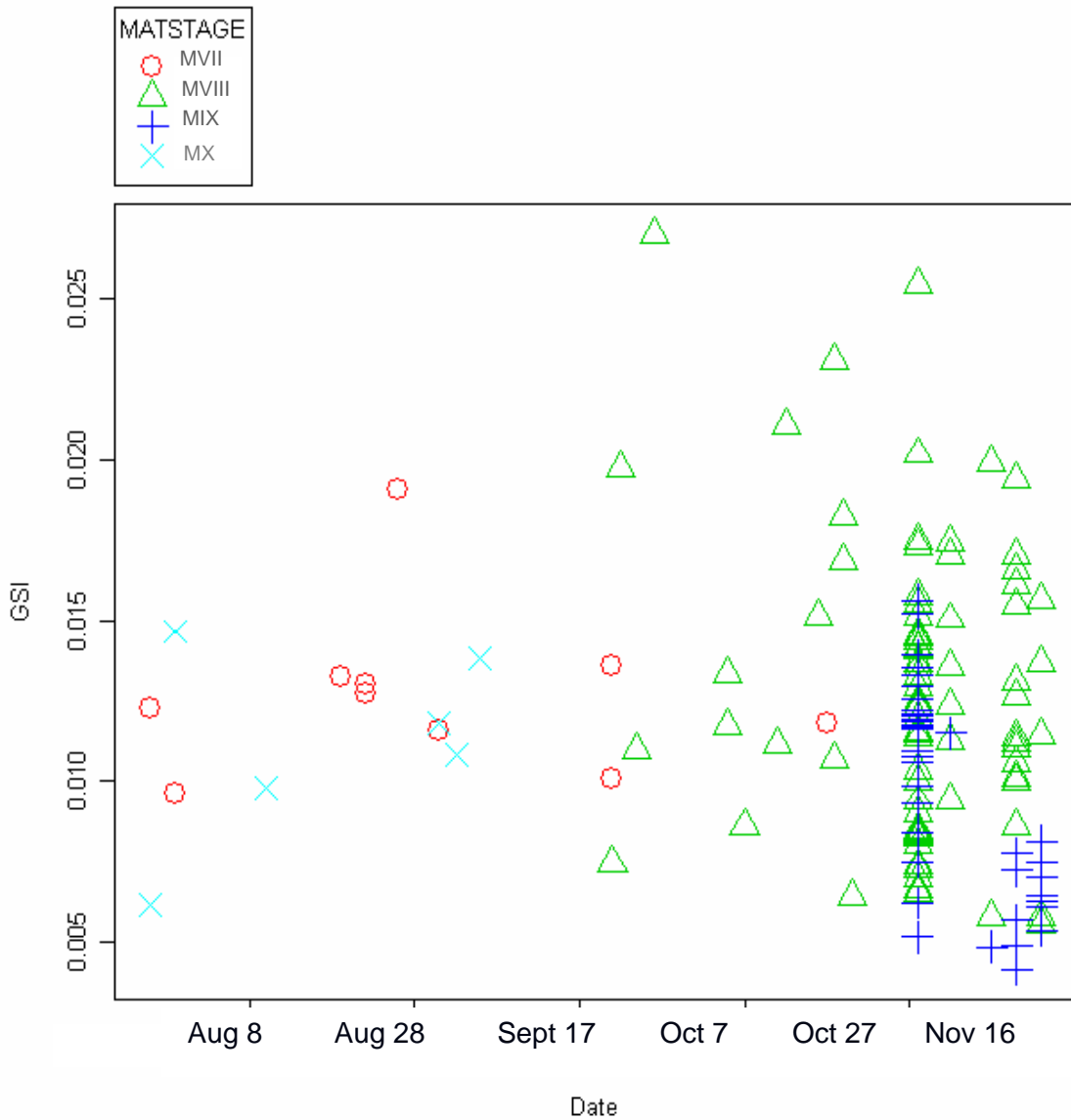


Figure 10: Graph of the GSI by date of male Broad Whitefish captured in the Arctic Red River in 1993. The individual fish are categorized by maturity stage from the visual observation in the field. Mature males (M7) = O; ripe males (M8) = Δ; spent males (M9) = +; and resting males (M10) = x.

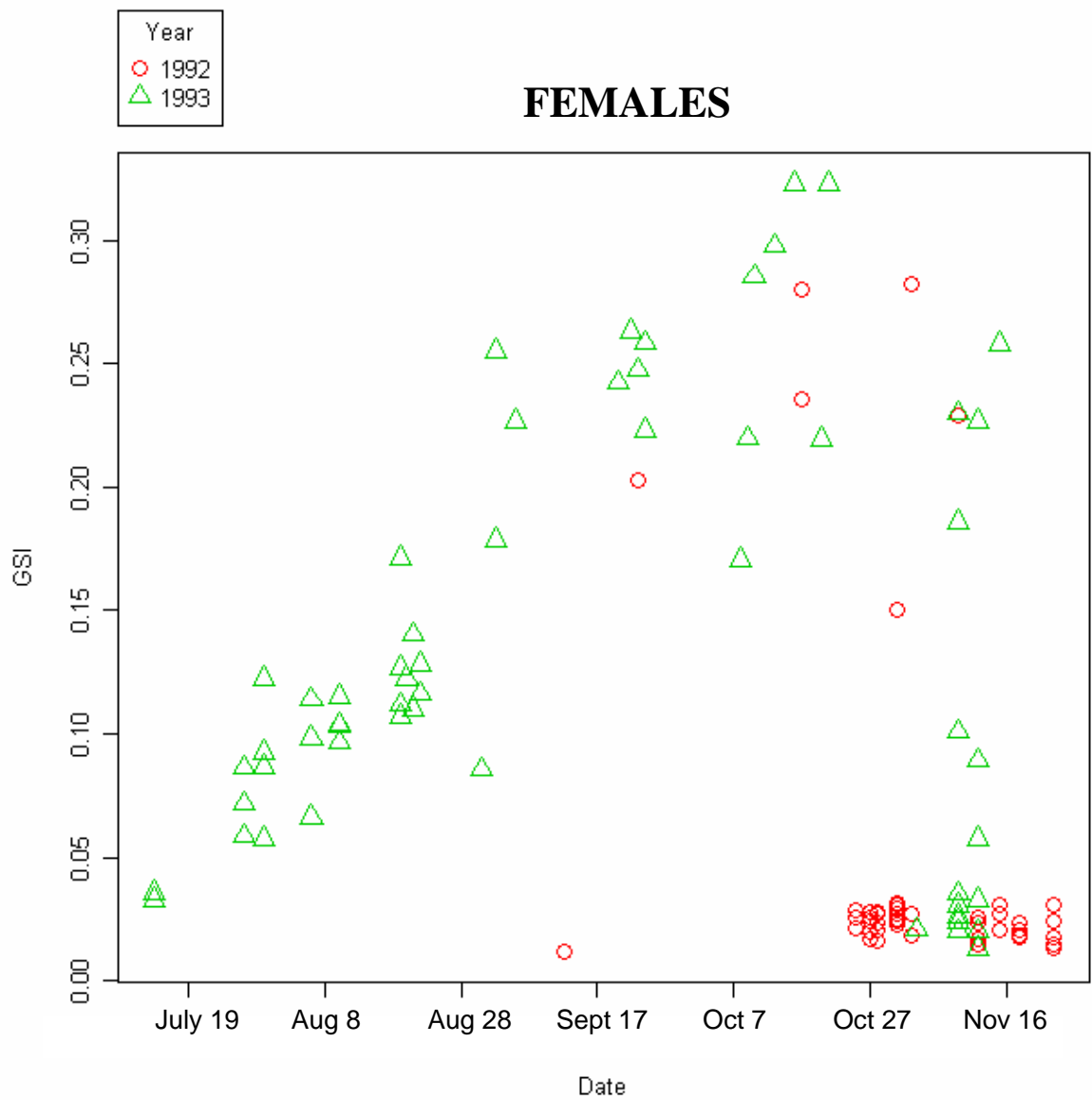


Figure 11: Scatter plot of GSI for migrating female Broad Whitefish in the Arctic Red River during 1992 and 1993.

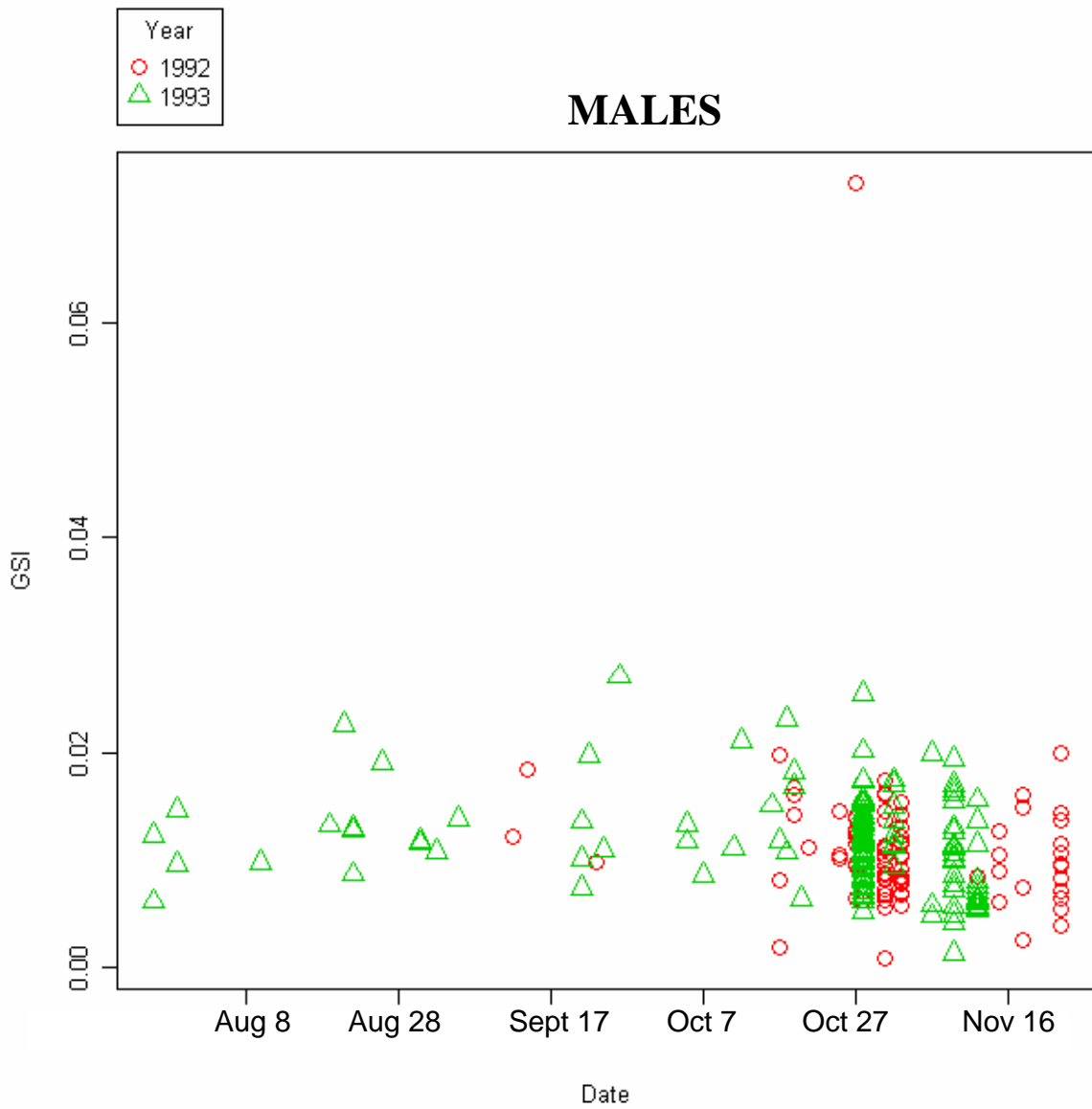


Figure 12: Scatter plot of GSI for migrating male Broad Whitefish in the Arctic Red River during 1992 and 1993.

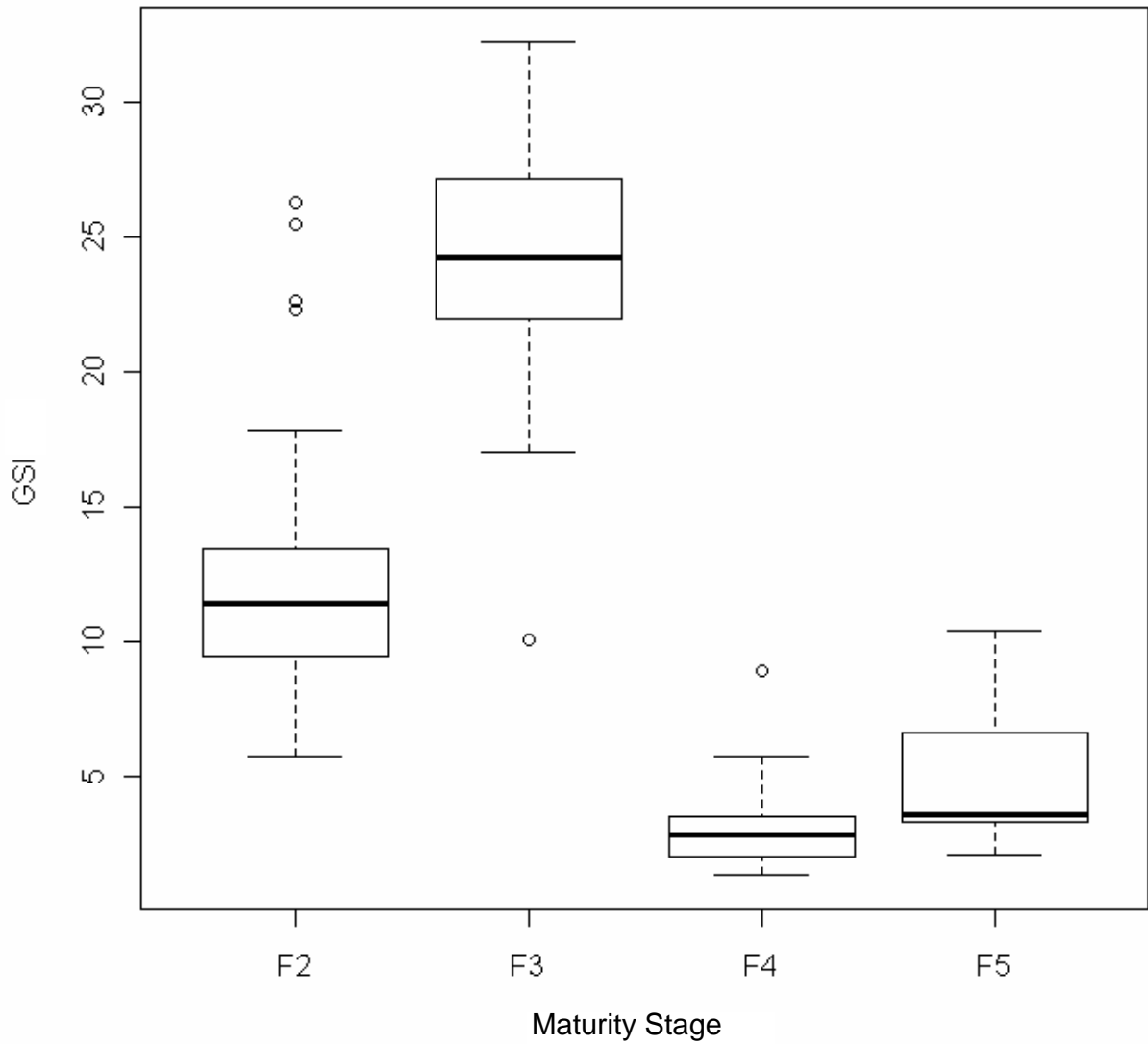


Figure 13: Box plot of the GSI related to maturity stage for female Broad Whitefish captured in 1993. Coding for the maturity stage F2: Female Mature, F3: Female Ripe, F4: Female Spent, and F5: Female Resting. The thick black line within the box represents the median of the data, the top of the box represents the 25<sup>th</sup> percentile, and the bottom of the box represents the 75<sup>th</sup> percentile. The vertical dashed lines represent 1.5 times the interquartile range of the data and the circles represent individual outliers to this range.

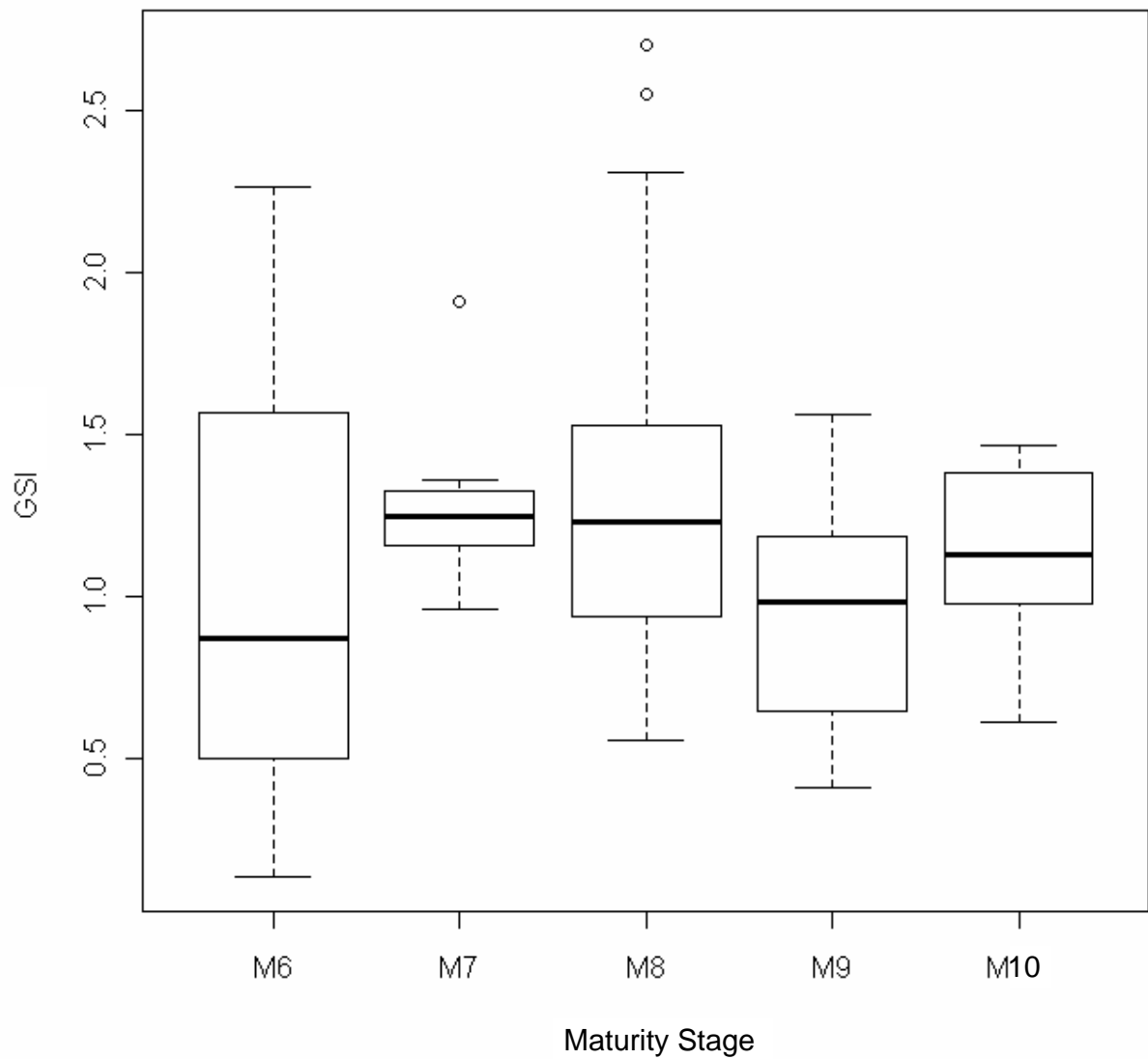


Figure 14: Box plot of the GSI related to maturity stage for male Broad Whitefish captured in 1993. Coding for the maturity stage M6: Male Immature, M7: Male Mature, M8: Male Ripe, M9: Male Spent, and M10: Male Resting. The thick black line within the box represents the median of the data, the top of the box represents the 25<sup>th</sup> percentile, and the bottom of the box represents the 75<sup>th</sup> percentile. The vertical dashed lines represent 1.5 times the interquartile range of the data and the circles represent individual outliers to this range.



### *Correlations between timing and purpose of migration*

The results for the GLM show sporadic correlation between date and CPUE with the two different measures of maturity (Appendix L). For male Broad Whitefish date was found to be correlated to GSI in the GLM that applied to data from mid-October to mid-November. Date was not found to be correlated to GSI in any other GLM. For female Broad Whitefish date was found to be correlated to GSI in the GLM applied to the data from before October 30<sup>th</sup> and specifically in the GLM applied to the data between July and September. For male Broad Whitefish date was found to be correlated to maturity stage in the GLM applied to all the data and in the GLM applied to the before Oct 30<sup>th</sup> data. For female Broad Whitefish date was found to be correlated to maturity stage in only the GLM that applied to all data. For male Broad Whitefish CPUE was found correlated to GSI by the GLM applied to before Oct 30<sup>th</sup> and specifically to the GLM applied to data from mid-October to mid-November. For female Broad Whitefish CPUE was found correlated to GSI in the GLM that applied to all the data. For both male and female Broad Whitefish CPUE and maturity stage were never found to be correlated. All this comes together to indicate that the correlation between date and CPUE with measures of maturity (GSI and maturity stage) is limited to the strict time window within which Broad Whitefish are migrating.

### *Migration Characteristics - Logit Model*

In this study the assignment of maturity stages was inconsistent and sparse in 1992, leading to the removal of 1992 data from the cumulative logit model of maturity stage (Appendix I). The cumulative logit model was executed for each sex independently. The logit model was run for all possible combinations and each model was compared using AIC. Since the sample sizes for female and male maturity models are above  $n = 40$ , it is not necessary to use the corrected AIC (AIC<sub>c</sub>) (Bolker 2008).

### Logit Model – Females

Due to low sample sizes of resting (F5, n = 5) and spent (F4, n = 10) fish, the two maturity stages were combined for the purpose of modelling. The Logit Model requires a minimum sample size of 5 per category but works best with greater sample sizes in every category (Stokes *et al.* 2009). The female maturity categories used in the model were: mature (F2, n = 27), ripe (F3, n = 24) and resting/spent (F4.5, n = 15). When maturity categories are combined for the purpose of modelling the biological implications of combining categories must be considered. Within this model, it is assumed that resting and spent female fish will have the same gonad weight and GSI; therefore, they are categorized as the same, despite the biological differences of the maturity stages.

The results from the AIC test show that model #3 with predictor variables are GSI and date, (Table 4) is the best fit for the female data. It should be noted that there was a difference of 4 between the  $\Delta$ AIC values of the full model (model #1) and model #3. A difference of 4 or more  $\Delta$ AIC values is commonly accepted to consider the models distinguishable but close enough in common that both should be considered reasonable in fit (Bolker 2008). According to the AIC scoring it is the model with the lowest score (with a difference of 4 or more) that is deemed best fitting among the tested models, but all models with  $\Delta$ AIC values of 10 or less should be considered similar to each other and pretty good fits to the data (Anderson 2008).

The results from the Global Null Hypothesis test (Table 5) show that the fit of the model is reasonable for the data, as the likelihood ratio test is non-significant with a value of 95.7046 with 4 df and the score test has a non significant value of 68.7858 with 4 df. The Type III Analysis of Effects shows that GSI has an overall (cumulative) influential effect on maturity stage ( $Pr > Chi Sq = 0.0148$ ), while date does not have an overall (cumulative) influential effect on maturity stage ( $Pr > Chi Sq = 0.1225$ ). Despite the cumulative effect being greater than  $p = 0.05$  the individual

effects (influence of date at each comparative category) are closer to the boarder line (F3 vs. F2  $p = 0.0980$ ; F 4.5 vs. F2  $p = 0.0728$ ), thus the variable date should be kept in the logit model for female groups.

### Logit Model – Males

Due to low sample sizes of immature males (M6,  $n = 3$ ), immature and mature groups (M7,  $n = 10$ ) were combined. In addition there were low sample sizes of resting males (M10,  $n = 6$ ) so resting and spent (M9,  $n = 42$ ) were combined. The male maturity categories used in this model were: immature/mature (M6.7,  $n = 13$ ), ripe (M8,  $n = 84$ ) and spent/resting (M9+,  $n = 48$ ). Due to the need to combine some of the maturity categories for the purpose of modelling, the results will not provide information on the immature, mature, spent and resting fish individually. The immature and mature category (M 6.7) must be interpreted biologically with caution as there are two biologically distinct phases of maturity combined into one. This is the same for the category that combines spent and resting males (M9+). It is expected that despite these limitations of the model due to combining categories, the output will be valuable for the purpose of looking at ripe males compared to the two other categories, as the ripe males are of most interest to this research.

Like with the females, the results from the AIC test show that the full model (model # 1) and model #3 (Table 4) should both be considered good fits. However, unlike the females the difference between their  $\Delta AIC$  values is 1.36, indicating that both models are distinguishable one from the other but that neither can be strictly determined better than the other (Bolker 2008). Thus, model #1 and model #3 are both considered best fitting for predicting male maturity. This indicates that the predictor variables needed to predict male maturity are definitely GSI and date and maybe CPUE. The presence of CPUE in the predictor model indicates that males may migrate in mass congregation as figure 9 and figure 12 illustrate; however, the statistical evidence supporting this is weak.

The results from the Global Null Hypothesis (Table 6) test shows that the likelihood ratio is not significant with a value of 65.4204 with 6 df and the score test is not significant with a value of 76.7084 with 6 df. From this information it is concluded that the fit of the model is reasonable for the data. The Type III Analysis of Effects shows that GSI and date have overall influential effects on maturity stage ( $\text{Pr}>\text{Chi Sq} = 0.0002$ ,  $\text{Pr}>\text{Chi Sq} = <0.0001$ , respectively) while CPUE does not ( $\text{Pr}>\text{Chi Sq} = 0.1909$ ). Despite CPUE not having a significant effect at the overall level (Type III Analysis of Effects) nor at the individual comparative level (Analysis of Maximum Likelihood Estimates) the results from the AIC test (Table 4) and figure 9 and figure 12 indicate that this variable (CPUE) should be kept in the model.

Table 4: Logit model AIC results for modelling Broad Whitefish maturity stage using up to 3 variables (GSI, CPUE, DATE) for the migration of Broad Whitefish in the Arctic Red River, NWT.

*Females*

<b>Model Number</b>	<b>Variables</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Model #1 (Full Model)	GSI, CPUE, DATE	40.401	3.66
Model #2	GSI, CPUE	64.217	27.47
Model #3	GSI, DATE	36.745	0
Model #4	GSI	60.413	23.67
Model #5	CPUE, DATE	82.567	45.82
Model #6	CPUE	114.002	77.26
Model #7	DATE	91.974	55.23

*Males*

<b>Model Number</b>	<b>Variables</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Model #1 (Full Model)	GSI, CPUE, DATE	211.131	0
Model #2	GSI, CPUE	239.980	28.85
Model #3	GSI, DATE	212.491	1.36
Model #4	GSI	250.930	39.80
Model #5	CPUE, DATE	229.218	18.09
Model #6	CPUE	253.633	42.50
Model #7	DATE	230.256	19.13

Table 5: Logit model #3 results for 1993 females (reference F2)

Response Profile

<b>ORDERED VALUE</b>	<b>MATSTAGE</b>	<b>TOTAL FREQUENCY</b>
1	F2	27
2	F3	15
3	F4.5	15

Testing Global Null Hypothesis: Beta = 0

<b>TEST</b>	<b>CHI-SQUARE</b>	<b>DF</b>	<b>PR&gt;CHI SQUARE</b>
Likelihood Ratio	95.7046	4	< 0.0001
Score	68.7858	4	< 0.0001
Wald	8.6210	4	0.0713

Type III Analysis of Effects

<b>EFFECT</b>	<b>DF</b>	<b>WALD CHI-SQ</b>	<b>PR&gt;CHI SQUARE</b>
GSI	2	8.4214	0.0148
Date	2	4.1990	0.1225

Analysis of Maximum Likelihood Estimates

<b>PARAMETER</b>	<b>MATSTAGE</b>	<b>DF</b>	<b>ESTIMATE</b>	<b>STANDARD ERROR</b>	<b>WALD CHI-SQ</b>	<b>PR&gt;CHI-SQ</b>
GSI	F3	1	0.3185	0.3437	0.8584	0.3542
GSI	F4.5	1	-0.9640	0.3703	6.7770	0.0092
Date	F3	1	0.1879	0.1136	2.7381	0.0980
Date	F4.5	1	0.0793	0.0442	3.2178	0.0728

Table 6: Logit model #1 results for 1993 males (reference M6.7)

Response Profile

ORDERED VALUE	MATSTAGE	TOTAL FREQUENCY
1	M6.7	13
2	M8	84
3	M9+	48

Testing Global Null Hypothesis: Beta = 0

TEST	CHI-SQUARE	DF	PR>CHI SQUARE
Likelihood Ratio	65.4204	6	< 0.0001
Score	76.7084	6	< 0.0001
Wald	36.6251	6	<0.0001

Type III Analysis of Effects

EFFECT	DF	WALD CHI-SQ	PR>CHI SQUARE
GSI	2	17.0268	0.0002
CPUE	2	3.3116	0.1909
Date	2	19.9011	<0.0001

Analysis of Maximum Likelihood Estimates

PARAMETER	MATSTAGE	DF	ESTIMATE	STANDARD ERROR	WALD CHI-SQ	PR>CHI-SQ
GSI	M8	1	1.3859	0.9473	2.1405	0.1435
GSI	M9+	1	-1.0821	0.9962	1.1797	0.2774
CPUE	M8	1	2.0686	1.6676	1.5386	0.2148
CPUE	M9+	1	2.4211	1.6718	2.0972	0.1476
Date	M8	1	0.0658	0.0147	19.8796	<0.0001
Date	M9+	1	0.0347	0.0122	8.1192	0.0044

## DISCUSSION

### *Timing of Migration*

In 1992 and 1993, there was a migration of Broad Whitefish in the Arctic Red River from mid-October to early November. This is supported by the increased abundance (CPUE) of Broad Whitefish in gill net catches. Traditional knowledge of local Gwich'in people from the community of Tsiigehtchic located on the Arctic Red River support that there is an increase in abundance of Broad Whitefish during October and November (Greenland and Walker-Larsen 2001). Tagging work completed by Chang-Kue and Jessop (1991), Babaluk *et al.* (2001) and Howland *et al.* (2009), corroborate these findings. The tagging data indicates that Broad Whitefish populations move from overwintering grounds in early summer (late June, early July) and move upstream in the Arctic Red River until late October and early November (Chang-Kue and Jessop 1991). These previous studies, along with the data presented here, is strong evidence that there is an annual migration of Broad Whitefish in the Arctic Red River.

### *Purpose of Migration*

My findings from the maturity and GSI data demonstrate that the purpose of the Broad Whitefish migration in the Arctic Red River is for spawning. The visual assessment of maturity stage and GSI of migrating fish increased at the same time as abundance (CPUE), indicating that as abundance peaked more fish were in spawning condition. Further, there was a dramatic decrease in abundance of Broad Whitefish in early to mid-November which coincided with a maturity classification of spent or resting and decreased GSI. Together this information indicates that the Arctic Red River is an important spawning location for Broad Whitefish and that Broad Whitefish make a concerted migration during the fall to the spawning grounds.



### *Correlation between timing and purpose*

The GLM models illustrates the time of year where correlations between GSI and date with the measures of maturity were most present as being between approximately October and November, the same time that Broad Whitefish are migrating in the Arctic Red River and have elevated levels of GSI. This supports the fact that there is a strict time window within which Broad Whitefish migrate and spawn in the Arctic Red River.

These findings are supported by Traditional Knowledge of local people who capture what they term 'egg fish' during the fall (Greenland and Walker-Larsen 2001). Many other fish species are known to undertake migrations for the purpose of spawning because ideal spawning locations are typically not good juvenile and adult habitats (Brannon 1981, Miller and Brannon 1981). This is the first publication known to the author, that show empirical evidence that Broad Whitefish migrating up the Arctic Red River in the fall are in spawning condition.

These findings are similar to those found by VanGerwen-Toyne *et al.* (2008) on the Peel River, NWT. VanGerwen-Toyne *et al.* (2008) found that Broad Whitefish were the most abundant species captured in the Peel River and the abundance of Broad Whitefish increased from July to November. Parallel to my study VanGerwen-Toyne *et al.* (2008) noted that as Broad Whitefish abundance increased in the fall (September through November), so did GSI and visual maturity classification, indicating the presence of a spawning run. The timing of Broad Whitefish spawning migration in the Arctic Red River and the Peel River appear to be similar, between late October and early November (Stein *et al.* 1973, Chang-Kue and Jessop 1983, VanGerwen-Toyne *et al.* 2008). The reported date of highest abundance varies slightly, October 25<sup>th</sup> (VanGerwen-Toyne *et al.* 2008) to early November (Chang-Kue and Jessop 1983). This fluctuation may due to annual environmental changes, for example, warmer years should result in delayed migration runs, cold years should produce the opposite effect. The important consistency between all reports of Broad

Whitefish migration timing in the Mackenzie River system, including this study, is that spawning migration occurs under the ice annually sometime between mid-October and early November.

Notably, the water temperature at the time of Broad Whitefish migration and spawning was around 0.5°C. At these temperatures there is ice developed on the Arctic Red River and the silt has dropped from the water column. It may be biologically important that Broad Whitefish lay their eggs when there is little silt in the water column, as silt has been documented to suffocate and hinder egg production in other fish species (Lapointe *et al.* 2004, Levasseur *et al.* 2006).

All whitefish species are fall spawners in the Mackenzie River system (Table 1, McPhail and Lindsey 1970, Scott and Crossman 1973). This may be an adaptive trait for a number of reasons. The first is the decrease in suspended silt in the water. As water temperatures cool the silt in the water column drops to the bottom. It has been shown for other fish species that siltation present in the water column can reduce egg survival as siltation may cover the eggs and limit oxygen exchange between the egg and the aquatic environment (Levasseur *et al.* 2006). The second reason is decreased energy expenditure; as the Mackenzie River starts to freeze from the mouth to its headwaters, ice jamming causes water back-flowing which results in dramatically decreased water velocity (m/s) upstream in the Mackenzie River and associated tributaries like the Arctic Red River (Appendix J) (Lawford 1994, Environment Canada, Water Survey). Lastly, the extreme nature of the Arctic (e.g. spring floods, winters where rivers can be frozen solid) results in a short time window when fish can access spawning grounds that are geographically separate from favourable feeding and over-wintering grounds. In this system the corridor for fish to move from overwintering grounds to spawning grounds may only be open from July to November.

### *Migration Characteristics*

The logit model permits analysis to go beyond simple correlations between GSI, date and CPUE to provide information on the behaviour and characteristics of Broad Whitefish migration. The logit model showed that both timing (date) and gonad weight (GSI) are important for both sexes, indicating that Broad Whitefish need to arrive at the correct time to the spawning grounds, when other fish are there and prepared to spawn. The logit model showed that CPUE may be important to predict male maturity. This indicates that males may make a consorted run to the spawning grounds; these results are supported by the increased presence of male Broad Whitefish captured on October 27<sup>th</sup> with elevated GSI levels. However, the statistical evidence supporting CPUE as a variable in predicting male maturity is weak making the conclusion that males migrate in a mass weakly supported, and requiring more evidence. In contrast, the prediction of female maturity does not require the variable abundance (CPUE), indicating that females migrate to the spawning grounds in a continuous manner when permitted by water and environmental conditions (e.g. September to November).

As pointed out earlier, some maturity stages of both sexes needed to be combined to increase sample size and improve modelling results. The combination of spent and resting fish for both the females and males is likely not biologically important for the purpose of the model. It is unlikely that resting fish would expend this much time and energy on a migration to spawning grounds when they were not prepared to spawn. The GSI of spent fish is theoretically, and in practice often lower than resting fish, but by visual inspection the two maturity stages can appear very similar. The combination of male immature and mature maturity stages may be biologically problematic, as the distinction between immature and mature represents a shift in life stages from juvenile to adult (Stearns 1993). Similar to resting fish, it is unlikely that immature males would make a long and extensive migration to the spawning location, and not be prepared to spawn. Due

to the fact that the number of males classified as immature is low ( $n = 3$ ), this may be an error in the visual assessment of the maturity stage. Most of the maturity stages in males (e.g. immature, mature, resting and spent) can be difficult to differentiate because most changes are microscope and remain undetected macroscopically. The amount of change in GSI at different maturity stages of male Broad Whitefish is much lower than females supporting the idea that classifying maturity stages other than ripe is difficult in males and can lead to incorrect assessments.

Despite the limitations in the model it is clear that both male and female Broad Whitefish maturity stage is correlated with timing of migration and gonad weight. The link between GSI and maturity stage is directly related to more energy going to the creation of gonads, thus the weight of the gonads increases in proportion to the rest of the body (Wootton 1999). The link between timing of migration (date) and maturity stage indicate that there is a specific time window within which Broad Whitefish successfully spawn. Fish must be prepared to spawn when it is most advantageous environmentally and chance of success for off-spring is highest (Quinn 2005). Fish may use environmental cues as a way to synchronize gonad maturation with environment; for example, changes in food abundance, temperature, water chemistry or day length (light) may signal the development and maturation of gonads (Wootton 1999).

Broad Whitefish are able to optimize the environments of the Arctic which are patchy and disconnected by completing long migrations for the purpose of spawning indicating that Broad Whitefish have a life history that is well suited to the Arctic environment in which they persist. This study presents further knowledge on the migration timing and type of Broad Whitefish in the Arctic Red River. In addition, questions were unveiled regarding migration differences between female and male Broad Whitefish; these questions require more research in the future.

### **Chapter 3: Investigation into the role of water velocity on Broad Whitefish (*Coregonus nasus* (Pallas 1776)) habitat selection in the Arctic Red River, during spawning migration.**

#### **INTRODUCTION**

Habitat selection or niche selection is a topic of great interest within the field of fish ecology as it links behavioural ecology and population ecology. Habitat selection is defined as the process by which an organism selects a habitat depending on how well it meets the organism's survival needs (e.g. food, shelter, water, space) (Wootton 1999). There are numerous factors that attribute to habitat selection for fish; for example, water temperature (Heggenes *et al.* 1999), dissolved oxygen (Kramer 1987), substrate composition (Gotceitas and Brown 1993, Atkinson *et al.* 2004), cover (Boussu 1954, Fausch 1993, Allouche and Gaudin 2001), prey availability and predation (Allouche and Gaudin 2001, Atkinson *et al.* 2004, Folkestad 2005). All the factors combined result in fish selecting an appropriate habitat at any given time (Tyler and Clapp 1995). Within any aquatic environment fish must select the most suitable habitat. This can be challenging especially in highly variable and ever changing habitats like rivers.

Rivers are complex dynamic aquatic systems whose physical properties are constantly changing (e.g. volume, shape and size) over multiple time scales from momentary to millennial (Cushing and Allan 2001). Every physical factor of a river is linked and has a role in the forming and shaping of the river; however, for life in the rivers, current and current speeds are the most important factors (Giller and Malmqvist 1998). Current speed (water velocity) is the speed at which water moves in any small region of the river channel (Dodds 2002), and is affected by substrate type and water depth (Giller and Malmqvist 1998). Water velocity changes vertically and horizontally within the water column. On the vertical gradient water is typically fastest near the surface and slowest near the bottom (Hynes 1972). On the horizontal gradient water velocity is typically slowest near the banks and fastest near the centre (Dodds 2002). In addition to the spatial

variability of rivers, current speeds also change temporally, from hour-to-hour, and season-to-season (Pielou 1994). For example, during the spring many rivers experience flooding due to snow melt and run off (Pielou 1998). As water volume increases so too does water velocity, adding to the complexity of the river flow regime (Hynes 1972). Understanding the details and principles of water movement in rivers is critical to understanding fish habitat selection and fish movement within rivers.

Arctic rivers present difficult habitats for fish survival. Due to the extreme nature of the Arctic environment, Arctic rivers have four major hydrological events annually: snow melt, outflow at spring break-up, ice-free summer, and ice-covered winter (Sudgen 1982, Pielou 1994). These events can be limiting to fish habitat; for example the ice-covered winter may last for up to 8 months and the ice development can be deep enough to freeze rivers to the bottom (McBean 2005) either isolating fish upstream or forcing them to migrate downstream. Arctic fish species have developed numerous ways of adapting to their difficult and extreme environment, the most common adaptation is migration, specifically anadromy (Wrona *et al.* 2005). Anadromous fish divide their life cycle between freshwater and saltwater, experiencing most of their growth in saltwater while returning to freshwater for reproduction and spawning (Moyle and Cech 2004, McDowall 1997). Anadromous spawning migrations are physically demanding and therefore energetically expensive (Howland *et al.* 2000, Northcote 1982).

Water velocity has been noted as being one of the most influential factors for fish habitat selection as it directly and indirectly affects energy expenditure of a fish (Heggenes and Saltveit 1990, Nislow *et al.* 1999, Shivrell and Dungey 1983, Heggenes *et al.* 1996, Heggenes *et al.* 1999, Copp and Vilizzi 2004). Fast flowing water requires that fish expend more energy to remain stationary compared to slow moving water (Fausch 1993, Tyler and Clapp 1997); potentially resulting in lower survival with increased energy demands. In addition to requiring more energy to

remain stationary, fast flowing water may be a barrier to upstream fish passage if water speeds are too high for fish to swim against (Peake 2004, Colavecchia *et al.* 1998). In contrast, fast flowing water may provide more food resources for in-stream drift feeders. For example, water velocity has been reported as being the primary factor that determines habitat selection for juvenile Atlantic Salmon who are feeding in the rivers on prey items that drift by (DeGraaf and Bain 1986; Heggenes and Saltveit 1990). In addition to providing more energy supply via increased food resources, increased water velocity has been proposed to assist downstream migrating juvenile, reducing downstream migration energy demand (Gerking 1978).

As mentioned above, fast flowing water can be a barrier to fish movements in particular upstream fish migration. Migration is defined as the movement between one critical habitat and another (Roff 1992). There are many reasons that fish migrate, for example, following food, overwintering and spawning (Howland *et al.* 2000, Tallman *et al.* 2002). Migrations, particularly those for spawning, can be long travels where fish may expend large amounts of energy potentially limiting survival after migration (Leonard and McCormick 1999). For example, American Shad migrate up different rivers along the North American Atlantic coast, and depending on the degree of difficulty of the migration some populations do not survive after spawning (semelparous) and some do (iteroparous). Osborne (1961) proposed that it would be energetically ideal for upstream migrating fish to select paths with the lowest water flow; thereby conserving energy. Telemetry work done on migrating salmon identified current speed and flow turbulence as important environmental factors affecting migration path selection and energy use (Hinch and Rand 1998, Standen *et al.* 2002). Research with split-beam echosounders show migrating salmon swimming linearly along the banks and bottom of river systems (Xie *et al.* 1997) and in nearshore deep water, where flow is reduced (Ellis 1966). This demonstrates that salmon preferentially migrate in low velocity areas within river systems (Quinn 2005).

Research on the large scale migration of fish in Arctic rivers has been documented by tagging studies (Chang-Kue and Jessop 1991, Babaluk *et al.* 2001, Howland *et al.* 2009), and some traditional knowledge (Greenland and Walker-Larsen 2001, Thompson and Millar 2007). These reports only document the presence and timing of migrations along with prospective spawning locations. To my knowledge there has been no research completed that investigates the influence of water velocity on the selected migration path of upstream migrating Arctic fish.

The purpose of this study is to determine if Broad Whitefish in the Arctic Red River are selecting a specific habitat (water velocity) during their upstream migration to the spawning grounds. The objectives of this study are: 1) to determine if there is a difference in water velocity within the water column of the Arctic Red River, 2) if so, to determine if Broad Whitefish are selecting a specific habitat (in terms of water velocity) to occupy during the upstream migration to spawning grounds, and 3) to determine the swimming ability of Broad Whitefish to assess if there were parts of the Arctic Red River water column that would be barriers for fish migration.

To address the first objective, I took current profiles of the Arctic Red River. To address the second objective, I determined fish location in the river via the location of their capture in gill nets and then correlated the results with objective 1. To address the third objective I used swimming performance tests (fatigue tests) in a swim tunnel to develop a swim curve for Broad Whitefish.

Distinctively, this study examines habitat selection of an Arctic fish species during the time of fish migration. Additionally, the data for the swimming performance tests were completed in proximity to the natural environment (on the ice), at the time of the fish's natural spawning migration. In contrast, most swimming performance tests are completed in laboratories with hatchery or wild stocks at times and temperatures that may not represent the natural environment during migration.



## MATERIALS AND METHODS

### *Study Site*

The Arctic Red River, a tributary of the Mackenzie River, is the study site for this research. In 2007, field work for this research took place at a study site near the mouth of the Arctic Red River (Figure 15). Field data collection started October 15<sup>th</sup> and continued until November 12<sup>th</sup> with the exception of one week (October 30<sup>th</sup> to November 5<sup>th</sup>) where camp evacuation occurred due to warm weather thinning the ice and making field work on the ice unsafe. Multiple current profile measurements were completed over the same transect of the Arctic Red River where our net was set. The water temperature of the Arctic Red River at this time was 0.5°C with almost no fluctuation within the water column and from day to day. The silt in the river dropped, leaving the water clear.

### *Water Velocity in the Arctic Red River*

Current profiles were carried out on the Arctic Red River at the time of the spawning migration of whitefish species (October to November). Current profiling is a technique that measures the water velocity of a river cross section at numerous points along the vertical and horizontal plane, from which a 2D picture of water patterning and flow can be developed (Gore 2006). The Marsh-McBirney Flo-mate 2000 model was used; it is an electromagnetic current meter, for current profiling. An electromagnetic meter has the distinct advantage of recording negative water velocities (e.g. eddy lateral flow) (Gore 2006). Waddle (2007) used the Marsh-McBirney Flo-mate current meter to measure water velocity of the Cache la Poudre River, in Larimer County, Colorado, under the ice in January and found that this current meter offered the

best readings under the harsh conditions of winter weather (Terry Waddle personal communication, U.S. Geological Survey, Reston Virginia).

Current profiles were taken along the same transect that the net was set, as well as 5 m beyond. The net was first removed from the water to eliminate interference with water velocity readings. Current profiles were started at the nearest point to shore and 1 cm off the bottom. The probe was slowly placed into the water to minimize water disruption, sensor end facing upstream, to a maximum of 7.62 meters (cord length), or to 1 cm above the bottom, whichever came first. The meter was held in position for approximately ten seconds prior to reading water velocity, to allow for disrupted water to settle or pass by. The meter output a Fixed Point Average (FPA) every five seconds, meaning that an average of the water velocities measured was displayed every five seconds. The recorded value from the current meter was taken once the similar value appeared three times consecutively; this took about 20–40 seconds per measurement. Once a value was logged, the probe was gently raised to the next vertical interval (10 cm). This process was repeated for the entire vertical plane, until just below the ice. For surface readings taken just below the ice, the probe was fully submerged. Once an entire vertical profile was taken, the probe was removed from the water and moved to the next hole along the horizontal axis.

In total, current profiles along the same transect the net was set were measured four times throughout the field season. The measurements were completed immediately after the net was removed and fish were collected. Due to the limitation of daylight, current profile measurements could only be completed during the day time (approximately 10:00 am to 4:00 pm).

Current profile colour contour graphs were created using Sigma Plot 10.0.1, specifically a Renka computer algorithm was used to create the contour graphs.

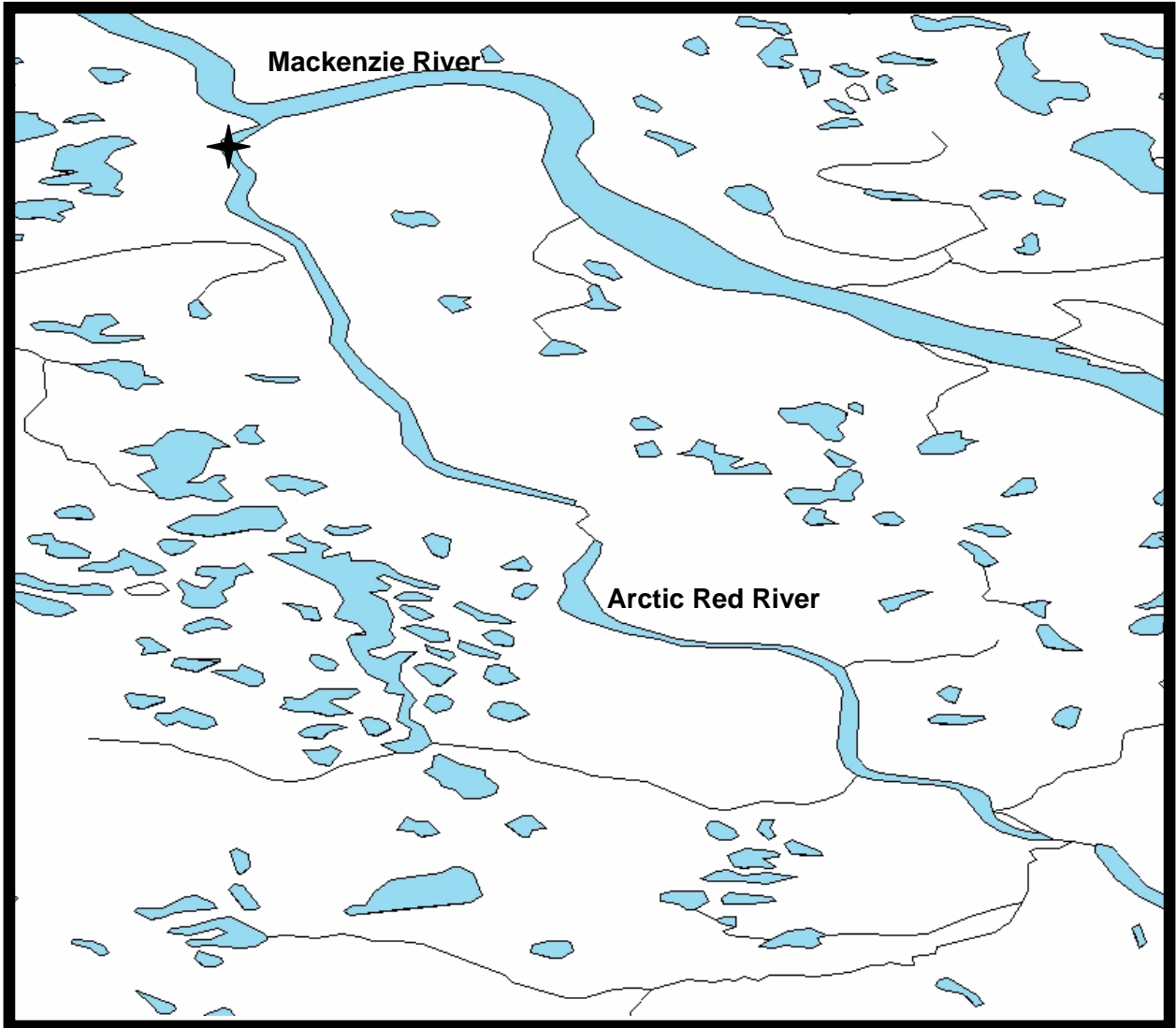


Figure 15: Map of the study site on the Arctic Red River in 2007, represented by ✦

### *Broad Whitefish Habitat Selection – Water Velocity*

Broad Whitefish were captured using gill nets that were 36.58 m long, 1.83 m tall, double leaded sink line and had four 9.14 m mesh panels of varying mesh sizes (11.43 cm, 8.89 cm, 10.16 cm, 7.62 cm - stretched mesh). The nets were set perpendicular to the shore in the main stream of the river, but not in an eddy. After ice freeze-up, nets were set under the ice using the willow branch method (Hubert 1996); this technique is similar to the traditional Gwich'in method used to set nets under the ice. The nets had to be set 1.8 m below the ice to ensure that the net would not become entrapped in the newly forming ice. The net was set along the same transect to allow for repeated measures of current profile and fish location to be collected. After each net set the net was reversed and re-set along the same transect. Reversing the net ensured that one mesh size was not in the same place in the river all the time, biasing the results of the catch data. When the nets were pulled, the location (x,y co-ordinates) of the fish in the net was measured, the fish were removed from the net and dead sampled for fork length (mm) and round weight (kg)m.

The physical location of the fish in the gill net was correlated to its position in the water column to determine the water velocity the fish were swimming against. To provide a mathematical analysis of the distribution I pooled the location data for all catches and compared the variance and the mean of Broad Whitefish distribution in the Arctic Red River.

### *Swimming Performance – Fixed Velocity Tests*

A fixed (fatigue) velocity test was used to construct a swim curve for Broad Whitefish. During this test, fish were exercised at a variety of fixed water velocities until exhaustion. This procedure was repeated for different sub-maximum swimming speeds (Hammer 1995). The data were compiled to construct a swimming curve, indicative of the average duration (length of time) a fish can swim at a given velocity. Swimming curves provide a more complete picture of a fish

species' swimming ability (Jones *et al.* 1973) compared to determining critical swim velocities ( $U_{crit}$ ), which tell only the maximum water velocity a fish can swim at for a given amount of time.

To assess the swimming ability of Broad Whitefish, a DT90 Qubit Systems swim tunnel was used. The DT90 swim tunnel has a test area of 70 cm x 20 cm x 20 cm (L x W x D), that is designed for trout-shaped fishes up to 1.5 kg (approximate fork length 500 mm) and has a flow range between 5 and 150 cm/s (Qubit Systems 2010). The water supply for the swim tunnel was pumped directly from the river through a hole in the ice by a submersible pump. Since the supply of water was abundant, a one-pass flow system was used.

Only undamaged and active fish were selected, carefully removed from the gill net (the net was cut if the fish was not easily removed), and taken immediately to the swim tunnel for a 60 minute acclimation period (Jones *et al.* 1974, Welch 1979). A water velocity of 0.35 m/s (a speed determined from preliminary laboratory experiments completed by Z Martin in 2006 at the University of Manitoba) was used during the acclimation period, as it initialized a rheotactic response. As the water used for the tests was the same water the fish was removed from, it was assumed that the fish were acclimated to the water temperature and properties. Thus, the acclimation period was used to enable the fish to adjust to the swim tunnel.

Once the acclimation period was complete, the water velocity within the swim tunnel was steadily increased to the test flow (between 0.4 and 1.30 m/s). Tests ended when either the fish was exhausted and remained on the back grate for 5 sec (after being encouraged to swim with sudden changes in water velocity) (Jones *et al.* 1974, Peake 2004), or at 120 min. According to Brett (1964), if a fish can swim for a maximum duration of 200 min, it is accepted as continuous swimming. Jones *et al.* (1974) used a maximum of 100 min for classifying continuous swimming in 100 m culverts. For this research, 120 min provided a slightly longer test than suggested by Jones *et al.* (1974), but still allowed for many fish to be tested within the short field season. Once

a test was finished, the water velocity was immediately returned to 0.35 m/s and the fish was left to rest for at least 10 min, measured then released. The swimming velocities tested were: 0.345 m/s, 0.425 m/s, 0.515 m/s, 0.555 m/s, 0.67 m/s, 0.775 m/s, 0.845 m/s, 0.93 m/s, 1.045 m/s, 1.105 m/s, 1.265 m/s and 1.305 m/s. The higher test velocity ( $> 1.045$  m/s) results were combined because it was difficult to get individual fish to swim at those velocities. For all other swim velocities at least 3 individual trials were completed to provide replication in the data set.

Fish in the swim tunnel were visually monitored for any signs of stress (e.g. excessive gill movement, thrashing, and rolling over). If a fish showed signs of stress, the water velocity was immediately dropped to 0.35 m/s and testing ceased. Once removed from the swim tunnel, round weight (kg) and fork length (mm) was taken.

## RESULTS

### *Water Velocity in the Arctic Red River*

Within the tested area of the Arctic Red River there is very slow flowing water during the time of Broad Whitefish spawning migration. The majority (72%) of the water velocity in the Arctic Red River is 0.0 m/s and 0.01 m/s at the time of Broad Whitefish migration (Figure 16). The highest water velocity measured in the Arctic Red River was 0.09 m/s. The distribution of water velocity was as follows: the slowest water near the banks and bottom of the river, the fastest water away from the banks and the bottom, but not at the surface (Figure 17). With the presence of ice on the river the water flow near the surface of the river is slowed dramatically due to the friction between the water and the ice. The fastest waters were found at depths of 0.5 m to 2.75 m and 10 m or more away from the river banks (Figure 17).

### *Broad Whitefish Habitat Selection – Water Velocity*

The 2-D location of Broad Whitefish in the water column, with correlating water velocity presented in Figure 18, demonstrates that Broad Whitefish do not migrate near the bottom of the river as expected but rather are distributed closer to the middle of the water column. Broad Whitefish were found to migrate in all water velocities that were present in the Arctic Red River, supported by Figure 19 illustrating the number of fish captured at the different water velocities and the proportion of the water column that each velocity comprises. This figure demonstrates that 78% of Broad Whitefish were swimming in 0.0 m/s (47%) or 0.01 m/s (31%) water when captured. These water velocities (0.0 m/s and 0.01 m/s) make up 72% of the water column (Figure 19). This leads to the idea that Broad Whitefish may be randomly distributed within the water column, and may not be selecting habitat for migration based on water velocity, statistical analysis needed.

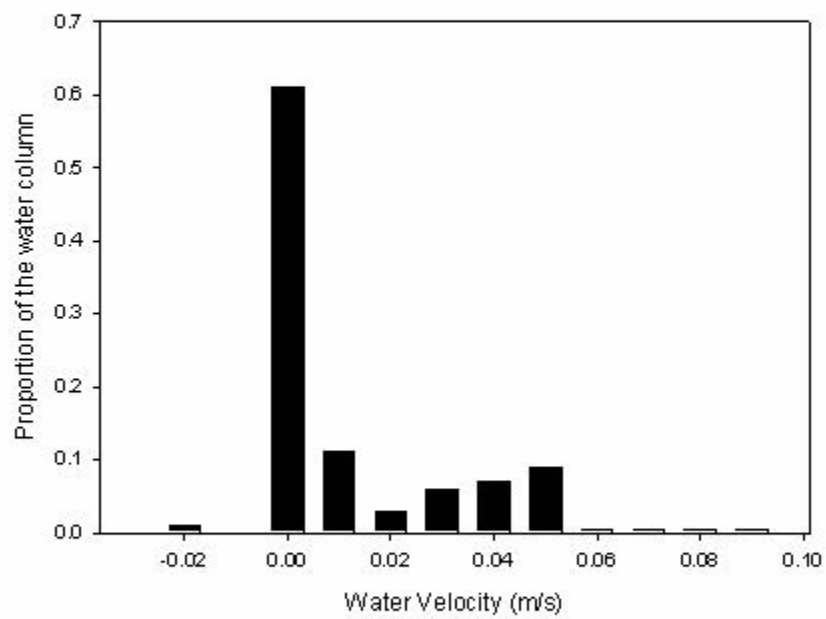


Figure 16: Range in water velocity (m/s) found at one site near the mouth of the Arctic Red River at time of Broad Whitefish migration, represented by the proportion of the river with that water velocity.



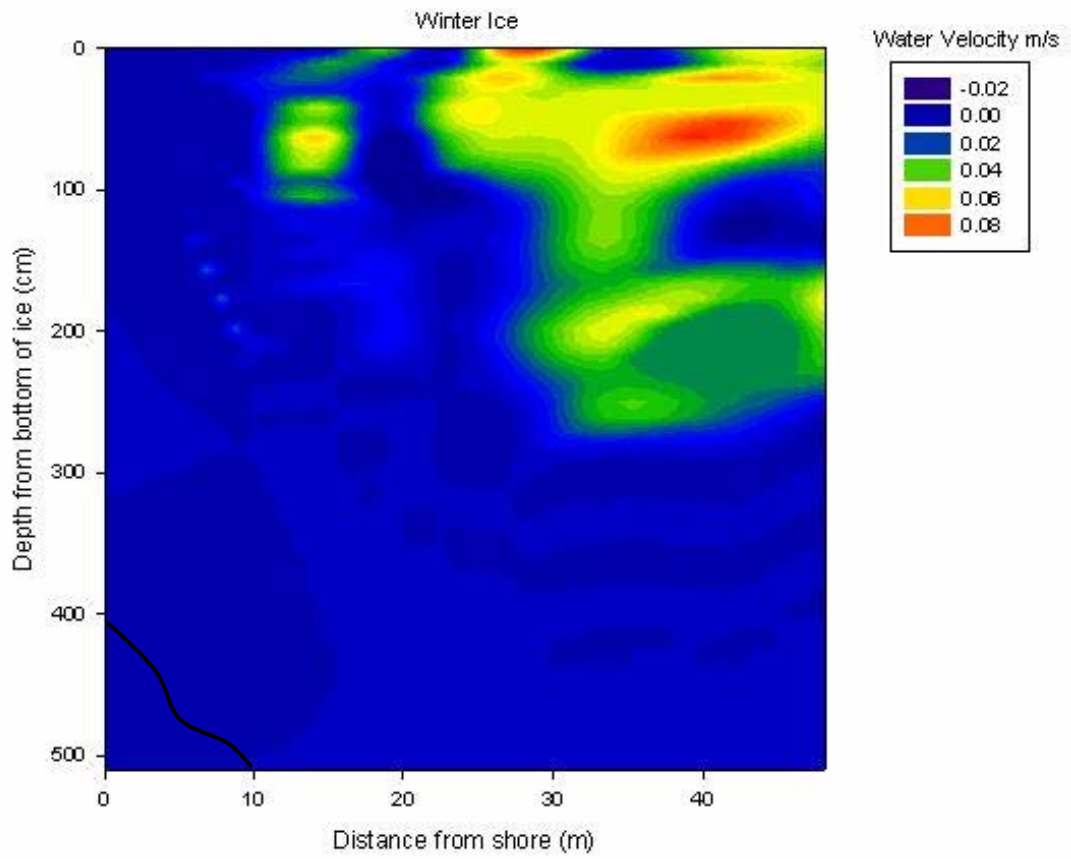


Figure 17: Current profile, a representative snapshot of the entire river section, of the Arctic Red River during Broad Whitefish spawning migration. Note that the water surface in this graph starts at the underside of the winter ice. The black line in the bottom left hand corner depicts the river bottom.

To provide a mathematical analysis of the looking at the available water velocities proportions and the water velocities Broad Whitefish were captured at I used a Chi-square analysis ( $\chi^2$ ) comparing the expected to the observed data. The null hypothesis is that the expected distribution (proportion of water velocity in the water column) and the observed distribution (proportion of Broad Whitefish captured at different water velocities) are homogeneous. For this test  $\alpha = 0.95$ , calculated  $\chi^2 = 9.69$  which is smaller than  $\chi^2_{tab0.95} = 11.070$ , allowing me to conclude that the two distributions are not different, fail to reject the null hypothesis. This supports the conclusion that Broad Whitefish are randomly distributed within the water column with reference to water velocity, indicating that Broad Whitefish show no preference to water velocity for migration in the Arctic Red River.

#### *Swimming Performance –Fixed Velocity Tests*

The water used in the swim tests was pumped from the Arctic Red River and was consistently  $0.5^\circ\text{C}$ , so the temperature for all swim tests was  $0.5^\circ\text{C}$ . The results show that there is high variability between the performance of individual fish at any given water velocity (Figure 20). There were 6 fish that swam for the full 120 min at the following water velocities: 0.345 m/s (1 fish), 0.425 m/s (2 fish), 0.555 m/s (1 fish), 0.725 m/s (1 fish) and 0.845 m/s (1 fish). These tests were excluded from the swim curve and subsequent analysis because it conveys the incorrect message to present fish exhaustion at 120 min, when the fish were not exhausted at 120 min. The accepted practice is to remove these trials from the analysis, report how many fish were removed and at what water velocity they were tested, since there is no feasible way to determine beyond the test period (120 min) the endurance time of the fish in these trials. The overall swimming endurance trend for Broad Whitefish decreased with increasing water velocity (Figure 20). When the swimming performance tests were averaged (Figure 21) the trend of decreasing endurance with

increasing water velocity becomes more evident, with an endurance outlier at water velocity 0.6 m/s. It appears that the swim speed of 0.6 m/s (~1.2 body length/second) has the highest endurance level for Broad Whitefish.

Larger fish size has been related to increase swimming endurance (Webb 1975). To examine if there was variance in swimming endurance in relation to fish size within the small range of Broad Whitefish tested, I plotted the fish length against endurance (Figure 22). A slight trend is observed for fish endurance to increase with increasing size; however, it should be noted that multiple water velocities were used limiting the conclusions of this graph.

The details of the individual swim test runs on the 29 successful Broad Whitefish are found in Appendix K. Notably, fish were tested at the different water velocities throughout the field season, ensuring a proper representation of random sampling for all swim abilities from all parts of the spawning run.

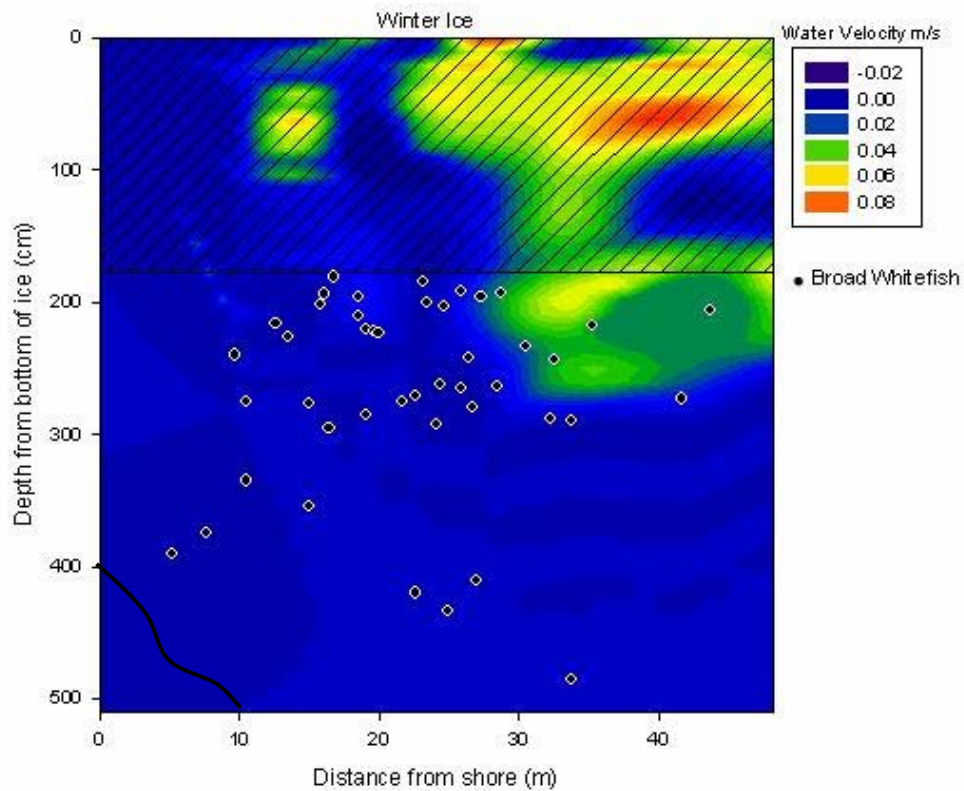


Figure 18: Location of Broad Whitefish captured in the Arctic Red River with associated water velocity (m/s) from the current profiles. Note that the hatched area at the top of the graph represents where the nets were not set. The nets were set 1.8 m beneath the ice to ensure that they would not freeze into the forming and reforming ice. The black line in the bottom left-hand corner depicts the river bottom in this area. This snapshot of the river represents part of the aquatic environment that Broad Whitefish encounter during their spawning migration.

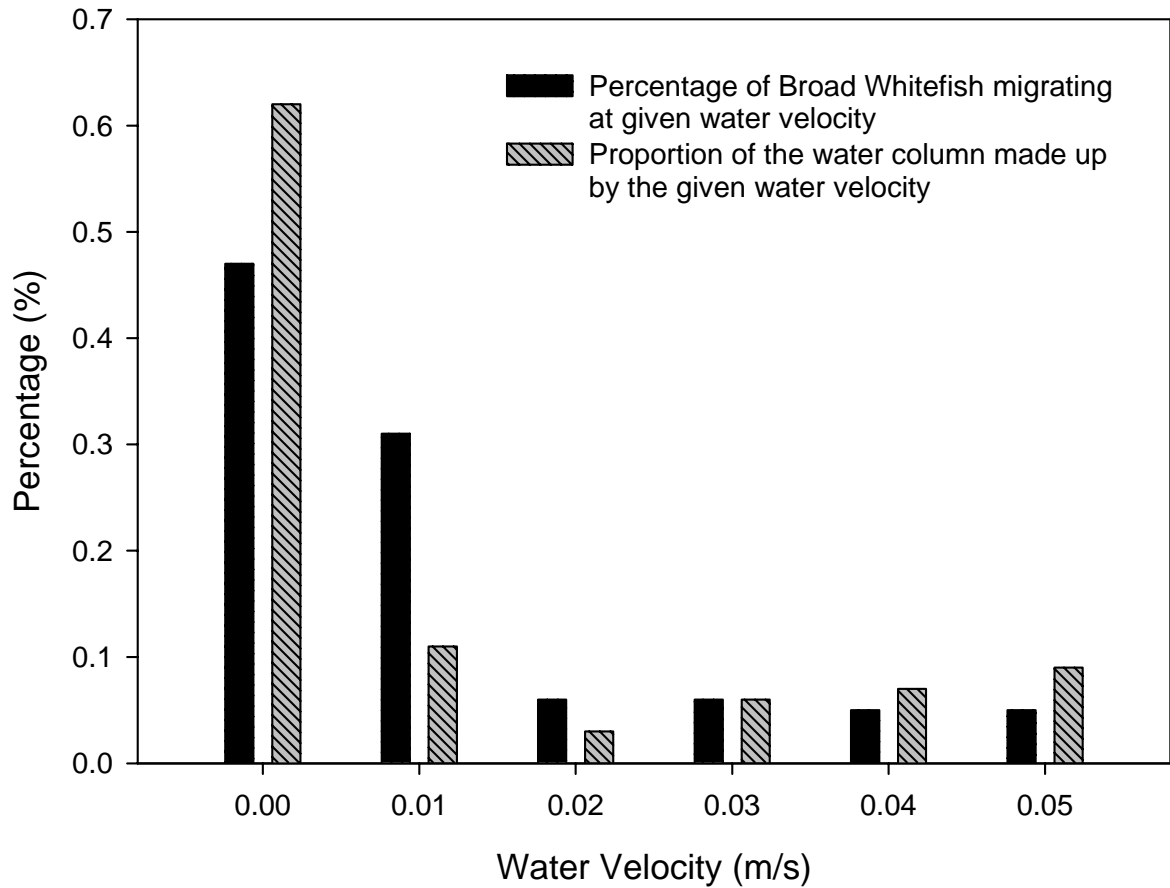


Figure 19: Number of Broad Whitefish captured at different water velocities (m/s) and the proportion of the water column made up by that water velocity, in the Arctic Red River, NWT.

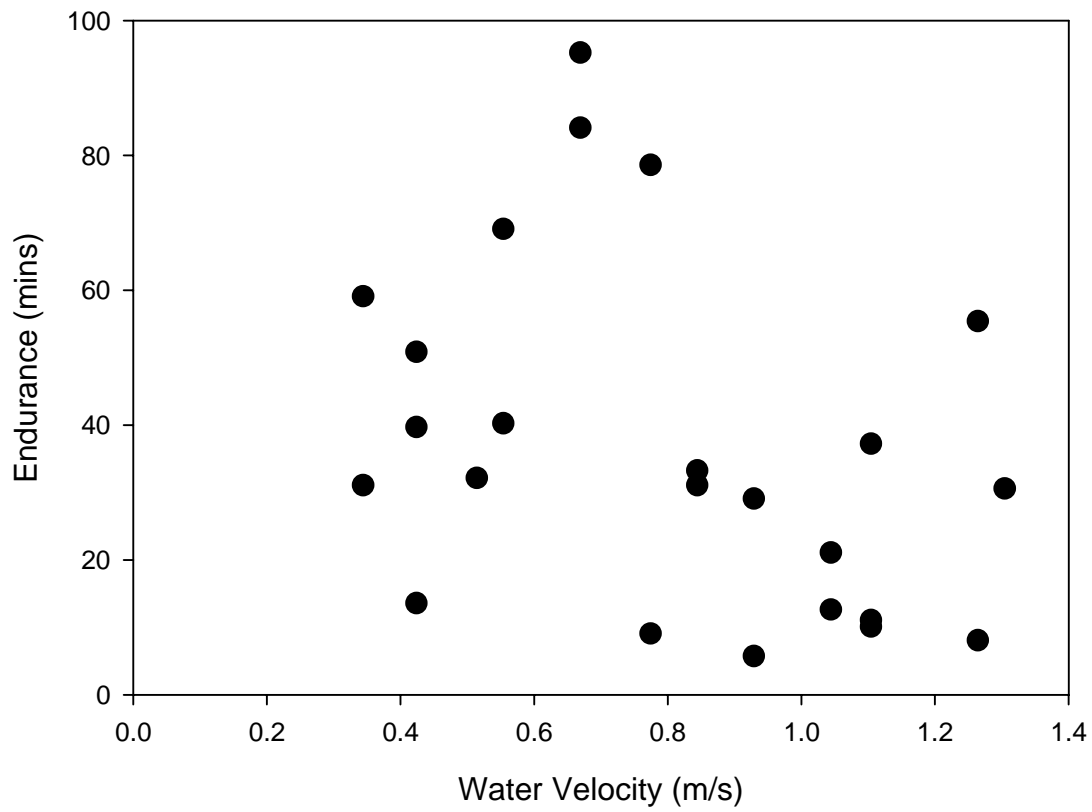


Figure 20: Endurance curve of Broad Whitefish from fatigue tests completed in the swim tunnel. The graph shows that as water velocity (m/s) increases time decreases.

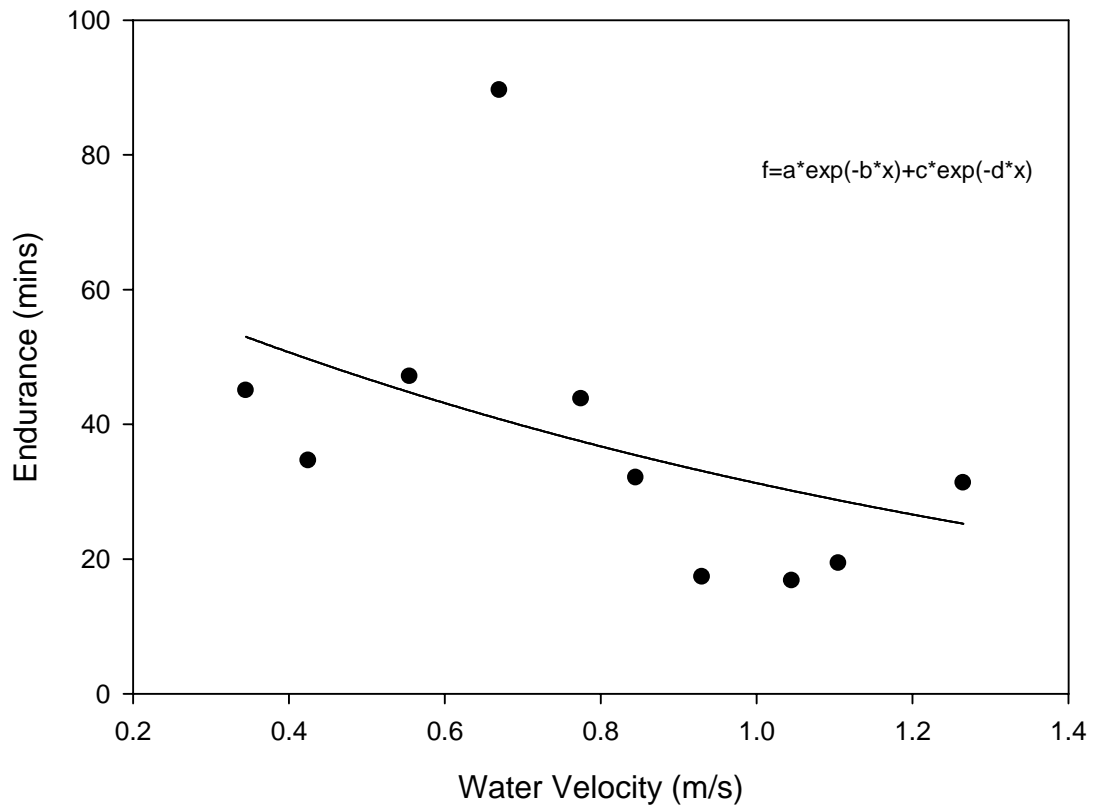


Figure 21: Average endurance time Broad Whitefish swam in fatigue tests at different water velocities. The trend line is an exponential line.

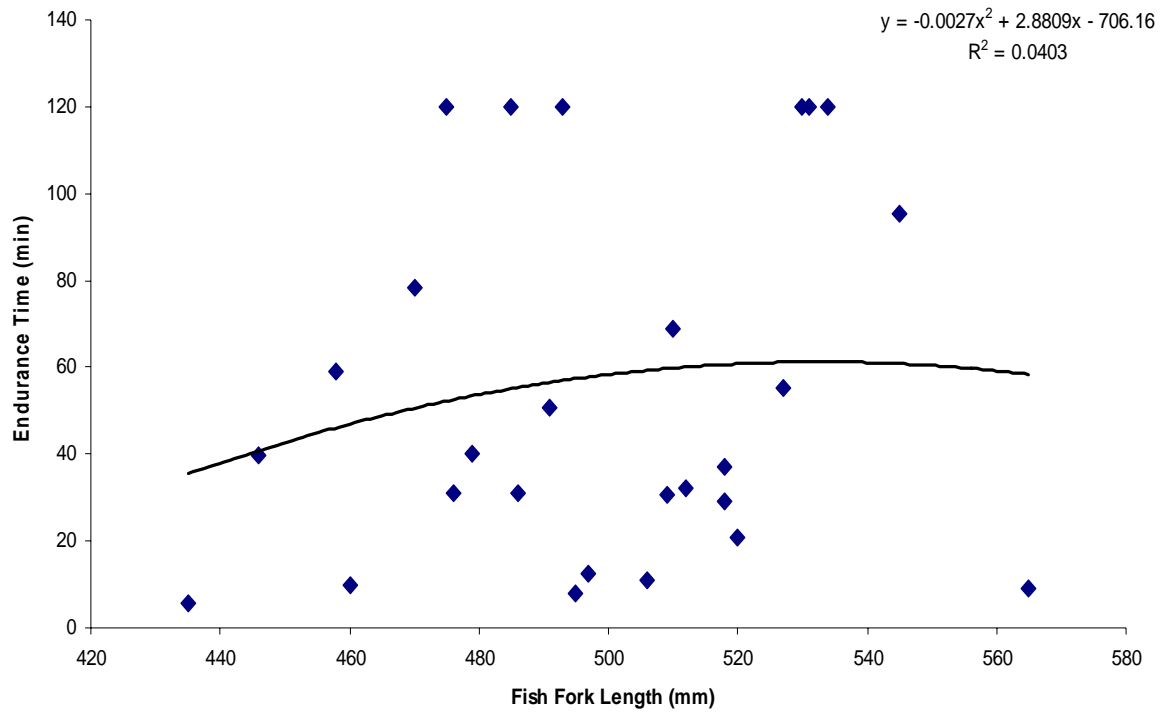


Figure 22: Comparison of the length of the fish to endurance of fish swimming across all tested water velocities of the fixed swimming performance tests. The test water velocities ranged 0.345 to 1.30 m/s. Note that the trials where fish swam for the full 120 were included in this graph. The trend line is an exponential function.



## DISCUSSION

As demonstrated in my study, discharge in the Arctic Red River is very slow at the time of Broad Whitefish migration. Habitat selection during spawning migration does not seem to be influenced by water velocity due to the uniform slow water in all available habitat. In addition, the swimming abilities of Broad Whitefish indicate that none of the Arctic Red River habitat poses a barrier to migration due to water velocity speed. Broad Whitefish can swim against water velocities 4 to 10 times higher than the velocities measured in the Arctic Red River at the time of migration. This information together indicates that Broad Whitefish do not appear to be limited in habitat selection by water velocity during their spawning migration in the Arctic Red River.

### *Water Velocity in the Arctic Red River*

The Arctic Red River has much lower water velocities than many temperate rivers at the same time of year. The water in the Arctic Red River at the time of Broad Whitefish migration is stagnant in many places (0.0 m/s and 0.01 m/s). This is most likely caused by the back-up of water in the Mackenzie River that occurs during freeze up. Back-up of water happens because, unlike southern rivers that freeze from their headwaters towards the mouth, the Mackenzie freezes from the mouth of the river south towards the headwaters causing flooding and water back-flowing upstream of ice jams and ice development (Sudgen 1982, Lawford 1994). Additionally, the Arctic Red River is a glacier fed river (Lloyd 1943, Tallman *et al.* 2002) and dropping temperatures cease the melting of the glacier reducing run off water to the river (Pielou 1998). A combination of these factors could explain the low water velocity measured in the Arctic Red River at the time of Broad Whitefish spawning migration.

### *Broad Whitefish Habitat Selection – Water Velocity*

In contrast to other spatial location studies, Broad Whitefish migrated near the center of the water column rather than close to the banks, this is likely attributed to the lack of variation in water velocity throughout the water column. Other species such as salmon species are known to swim during upstream migrations near the river banks or bottom (Hinch and Rand 1998, Quinn 2005). In parallel to other migrating fish species, salmon species are suspected to be travelling in areas with the lowest water velocity found where friction in the water column is the highest (banks and bottom). Since there is little difference in the water velocity through out the Arctic Red River, Broad Whitefish are not limited to the banks or bottom. In fact, when water velocity is low and consistent in the water column the river mimics a lake situation and it can be assumed that habitat is selected for reasons other than water velocity. Considering fish swimming biomechanics in a situation of low water velocity, it is not advantageous for fish to swim near the bottom or shore, as physical objects (e.g. bank, rocks, logs) limit the undulatory motion of the fish's body, in particular the amplitude of the fish's caudal fin is restricted thereby restricting propulsion (Webb 1975). Choosing the middle of the water column to migrate is advantageous for Broad Whitefish since they can utilize both low velocity waters and avoid physical obstructions in the river thus experiencing maximum propulsion capabilities.

Due to ice formation, the top of the nets were set at depth (1.8 m) and therefore I can only speculate that some of that region would have been available for migrating Broad Whitefish. However, due to the jagged nature of ice development in the Arctic Red River it is expected that fish would not come in direct contact with the underside of the developing surface ice. As well during this time, anchor and frazzle ice are developing in the water column (Pielou 1998). Anchor ice is a submerged ice formation that attaches to rocks and other objects in the water column. Anchor ice typically is a rough formation that can be harmful to fish (Hynes 1972). Due to bank

restriction of undulatory motion and potential ice damage to fish, it is likely that Broad Whitefish will have a more successful migration by travelling in the center of the water column.

### *Swimming Performance – Fixed Velocity Tests*

The swimming performance tests showed that Broad Whitefish are able to swim in a sustained manner at speeds 4 to 10 times higher than those measured in the Arctic Red River at the time of spawning migration. This is the first recorded study that tested the swimming performance of Broad Whitefish in the natural environment (water temperature 0.5°C) at the time of spawning migration. Jones *et al.* (1973) tested the swimming endurance (critical velocity) of 24 Broad Whitefish in a laboratory setting at water temperatures of 12-13°C using a range in water velocity of 0.10 m/s to 1.03 m/s.. Critical velocity is defined as the maximum water velocity a fish can swim at for a determined period of time. Jones *et al.* (1973) found a proportional relationship between critical velocity (cm/sec) and fish length (cm), as fish length increased so too did critical velocity. Jones *et al.* (1973) noted there was high variability in critical velocity for any given fish length. The research of Jones *et al.* (1973) determined the maximum water velocity Broad Whitefish can swim at for 10 mins, in order to estimate the maximum allowable water velocity passing through a culvert in which Broad Whitefish could successfully traverse. My research similarly demonstrates the same trend that Jones *et al.* (1973) found of increasing endurance with increasing fish length, across all water velocities and high variability within these results.

In my study, Broad Whitefish showed high variability in swimming endurance between individuals at the same test speeds. Likewise, Bernatchez and Dodson (1985) documented high variability in swimming performance of Lake Whitefish (*Coregonus clupeaformis*). Despite the variability, the general trend in swimming performance of Broad Whitefish was decreasing endurance with increasing water velocity.

As documented with other fish species (Bernatchez and Dodson 1985), Broad Whitefish may have an optimal swim speed found at water velocities of approximately 0.6 m/s equalling about 1.2 body lengths per second ( $L/s$ ). Weihs (1973) and Videler (1993) noted that the optimal swimming speed across species was between 1.0 and 1.2  $L/s$ . This is indicative that the most energetically favourable swimming, both physiologically and behaviourally, for Broad Whitefish occurs at swimming speeds of 1.2  $L/s$ , resulting in maximum endurance for minimum effort.

Limitations to swimming performance tests, in particular forced swimming tests as I used in my study, assume that all fish will swim to maximum endurance at maximum speeds (Peake 2004). In reality, fish in forced swim tests will not swim at their optimal level due to a combination of things: behavioural refusal to swim, restriction of fin amplitude resulting in decreased force per tail beat (Webb 1975), and the inability to use energy saving strategies (Peake 2008). In general, forced swim tests underestimate the swimming potential of a fish. Despite limitations, forced swim tests are widely accepted and used as a research tool to best determine fish swimming abilities since the alternative options are extremely expensive, non-transportable and unrealistic for extreme environments like the Arctic.

A study by Chudobiak (1995) looked at the body morphology of two populations of Broad Whitefish in the Mackenzie River system, Arctic Red River and Travaillant Lake, to test if distance of migration influenced body shape. Chudobiak (1995) theorized that Broad Whitefish from Travaillant Lake would not migrate long distances compared to Broad Whitefish from the Arctic Red River, therefore the Arctic Red River population should have a body morphology more streamlined for migration. Broad Whitefish from Travaillant Lake are known to be land-locked for most of the year due to ice development (Chudobiak 1995); whereas, the Arctic Red River population is known to migrate extensive distances between over-wintering grounds, feeding grounds and spawning grounds (Chang-Kue and Jessop 1991). Chudobiak (1995) found no

significant difference between the body morphology of Travaillant Lake and Arctic Red River Broad Whitefish populations. In addition, Bernatchez and Dodson (1985) noted that comparisons of coregonid and salmonid swimming stamina suggest that whitefish migration is not an influential factor in the selection of body morphology. My current profile data suggests that the aquatic environment at the time of Broad Whitefish migration and other whitefish migrations is more similar to a lake than a river thus providing an explanation for both Chudobiak (1995) and Bernatchez and Dodson's (1985) conclusions. This would explain why Broad Whitefish in the Mackenzie River System do not show the characteristic hydrodynamic efficient body selection (e.g. tuniform body shape) of salmonids who travel upstream in fast flowing rivers like the Fraser River in British Columbia, Canada.

Broad Whitefish are well adapted to the environment in which they migrate. This study indicates that migration may occur annually at times when their habitat selection is not limited by fast water velocity and they are able to effectively swim at the low water temperatures. Broad Whitefish in the Arctic Red River, unlike other migrating anadromous fish species, are able to migrate away from the river bottom and banks of the river; allowing them full capabilities of swimming thrust locomotion. Furthermore, Broad Whitefish are able to swim against much faster water currents than are present in the river at the time of migration. Together this shows that Broad Whitefish are a well adapted anadromous Arctic fish species.

## Chapter 4: Discussion

### *General Summary*

The findings from this research conclude that Broad Whitefish undertook a spawning migration in the Arctic Red River in fall (mid-October to November), in 1992 and 1993. It is reasonable to assume that this spawning migration occurs annually in the Arctic Red River. The sexual maturation of Broad Whitefish appeared to be correlated to the time of year (date) and gonad-weight (GSI) for both sexes, while only male sexual maturation was correlated to abundance (CPUE) indicating that male and female Broad Whitefish may have different migration behaviours.

The Arctic Red River at the time of Broad Whitefish migration had very slow flowing water resembling a lake environment more so than a river environment. Broad Whitefish did not show a preference in water velocity for the purpose of migration in the Arctic Red River. This may be due to the fact that there is an abundance of slow flowing water and not a large difference between the fastest flowing waters and the slowest flowing waters, 0.00 m/s and 0.05 m/s respectively. Broad Whitefish in the Arctic Red River selected migration paths that were central in the water column; they did not appear to choose migration paths that were close to the banks nor the bottom of the river.

Swimming performance tests demonstrated that Broad Whitefish are physically able to swim at water velocities 4 to 10 times higher than those present in the Arctic Red River at the time of migration. Therefore, the migration path selected by Broad Whitefish is not limited by water velocity, and water velocity in the lower Arctic Red River is thus, not a barrier to fish migration.

### *Migration Timing in the Mackenzie River System*

The timing of fish migration is theorized to allow fish to optimize the spawning habitat and conserve energy on the migration (Roff 1982, Northcote 1978). From this research it appears that Broad Whitefish are well adapted to migrate in their Arctic environment. Compared with other anadromous whitefish species in the Mackenzie River System Broad Whitefish appear to be among the last to migrate up the spawning tributaries (migration occurs in mid-October through early November) and maybe the last whitefish species to spawn (spawning occurs in early to mid-November). Inconnu and Lake Whitefish species comprise the first whitefish spawning migrants in the Mackenzie River System. They have been documented migrating up spawning tributaries from July to late August and are theorized to spawn in September (Stein *et al.* 1973, Howland *et al.* 2000, VanGerwen-Toyne *et al.* 2008). Howland *et al.* (2000) reported that Inconnu captured in the Arctic Red River in early July to late August had elevated levels of GSI and fish captured in early October had low GSI indicating that spawning took place in September. Similarly, it is documented that Lake Whitefish captured in the Peel River have elevated GSI levels until early October (VanGerwen-Toyne *et al.* 2008). Female Lake Whitefish captured after October 1<sup>st</sup> were predominately post-spawners, indicating that spawning had occurred in September (VanGerwen-Toyne *et al.* 2008). Lastly, Least Cisco and Arctic Cisco migrate from late August to September and from early August to September, respectively (Stein *et al.* 1973, VanGerwen-Toyne *et al.* 2008). Least Cisco spawn in October and Arctic Cisco spawn October through November (VanGerwen-Toyne *et al.* 2008).

Further research similar to VanGerwen-Toyne *et al.* (2008), documenting the migration of all species in one tributary is needed, as the above information is compiled from different Mackenzie River tributaries. In addition, further research similar to that of Howland *et al.* (2000) comparing the variation in migration timing in one species between northern and southern

tributaries is needed to explore population adaptations to local environments. Lastly, there is a continued need for tagging studies of whitefish species in the Mackenzie River system similar to those conducted by Change-Kue and Jessop (1991), Babaluk *et al.* (2001) and Howland *et al.* (2009) as these studies provide information on movement, timing, environmental limitations, behaviour and general life history.

#### *Migration Timing, Water Discharge Levels and Swimming Performance*

Water discharge levels in the tributaries of the Mackenzie River are highest during spring flooding and decrease throughout the summer and the fall (Environment Canada, Water Survey, 2010). In the fall and early winter, discharge levels are extremely low and there is a potential for ice jams downstream in the Mackenzie River to create back-flowing water in the tributaries (Lawford 1994). Inconnu migrate upstream when discharge levels are high, compared with other whitefish species such as Broad Whitefish that migrate upstream when discharge levels are low. Inconnu are the largest of the whitefish species in the Mackenzie River System and they have a more tuniform body shape compared to Broad Whitefish allowing them to migrate far upriver into fast flowing waters (Scott and Crossman 1973, Howland *et al.* 2000). Lake Whitefish are one of the smaller whitefish species in the Mackenzie River System. They are more laterally compressed body than Broad Whitefish which may allow the Lake Whitefish to migrate in faster flowing water (Scott and Crossman 1973, Videler 1993). Least Cisco and Arctic Cisco are the smallest of the whitefish species in the Mackenzie River System and the ones with the most tuniform body shape which reduces drag on a fish's body allowing them to swim faster or against stronger currents (Scott and Crossman 1973, Webb 1975, Videler 1993). In contrast to Inconnu, Lake Whitefish, Least Cisco and Arctic Cisco, Burbot are a fish species that migrates in the Mackenzie River System after the Broad Whitefish migrations, their migration takes place in the



winter time (Scott and Crossman 1973). The migrations of Burbot populations in other northern countries have been studied and it was found that Burbot migrations coincide with very low water discharge levels (Slavik and Bartos 2002).

Jones *et al.* (1974) tested the critical swimming ability of several fish species found in the Mackenzie River System, including Broad Whitefish, Lake Whitefish and Inconnu and observed that Lake Whitefish and Inconnu have a higher critical swimming speed in comparison to Broad Whitefish. Lake Whitefish were found to have the highest critical swimming speed of the three species and were considered to be the strongest swimmers of the three species. Inconnu were considered to be stronger swimmers than Broad Whitefish, consistent with the observations that Lake Whitefish and Inconnu travel upstream when water discharge levels are higher. However, it should be noted that the maximum test velocities used by Jones *et al.* (1974) were about 1 L/s (0.60 m/s) which should not be a challenging swimming speed for any fish species (Brett 1964, Weihs 1973, Webb 1975). My research demonstrates that Broad Whitefish are able to swim at water velocities much higher than those Jones *et al.* (1974) tested suggesting that Broad Whitefish are strong swimmers. If Jones *et al.* (1974) underestimated the swimming abilities of all species tested, the comparative information between species that Jones *et al.* (1974) presented is accepted, but the maximum limits of the swimming potential for any of the species should be used with caution.

With increased industry development in the Arctic it is extremely important that more research on swimming potential of Arctic fish species is conducted. It is well accepted that salmon guidelines do not apply to Arctic fish species. Thus, culverts and bridges which disrupt water flow and currents cannot be developed using Pacific salmon guidelines; rather guidelines specific to Arctic fish species need to be developed.

### *Migration and Time Windows*

Distinct timing of migration for all coregonids in the Mackenzie River System is the result of the limited time windows that Arctic environments provide for successful completion of critical aspects of fish life cycles. The tributaries of the Mackenzie River have limited access time for migrating adult fish (July to November). Fish can only start to migrate upstream after spring floods, and migration returning downstream must be complete before winter potentially freezes portions of the rivers solid. This defined time window within which fish must migrate is a common trait found in many species (Brannon 1981, Miller and Brannon 1981). For example, in any given month there are Pacific salmon beginning their upstream spawning migration, but from population to population the timing of the migration is defined and specific (Quinn 2005). Specific timing of migrations permits fish populations to have individuals arrive at spawning grounds when the habitat is optimal for fitness and population survival (e.g. best time to spawn to give offspring the best chance at survival) (Northcote 1982, Quinn 2005). Broad Whitefish appear to be well adapted to utilizing the time windows of their Arctic environment. They migrate at a time that appears to be energetically optimal, spawn and then move back downstream before the rivers fully freeze. The offspring of Broad Whitefish emerge in the spring in the presence of floods waters and are carried directly to flourishing feeding grounds along the coast (Thera 1998) where the life cycle continues all over again.

### *Migration Behaviour and Energetics*

Broad Whitefish migration behaviour involves periods of active swimming followed by periods of holding position (Chang-Kue and Jessop 1991, Howland *et al.* 2009, Babaluk *et al.* 2001). This is a common trait exhibited by many anadromous fish (Leggett 1976, Edo and Suzuki 2003). A tagging study on Connecticut River American Shad by Leggett (1976) documented that

upstream migrating American Shad would meander, hold and even move downstream. In addition to Leggett's work, Edo and Suzuki (2003) describe the migration of Masu Salmon (*Oncorhynchus masou*) as having two migration periods with a rest period in between. The behaviour of meandering and movements downstream during upstream spawning migrations is considered to be energetically inefficient as fish are expending extra energy compared to directed travelling (straight line) (Leggett 1976, Bernatchez and Dodson 1987). In contrast, migrations that incorporate holding in a position, as exhibited by Broad Whitefish and Masu Salmon, are theorized to be more energy efficient. The fish migrate through the lower reaches of the river when it is optimal, then they wait in low velocity pools until the time is right to migrate in the upper reaches (Edo and Suzuki 2003). Winter and summer migrating Chinook Salmon exemplify migrations involving an extreme waiting period. Chinook Salmon winter and summer migrants enter freshwater with immature gonads, and hold position in the river for months prior to fall spawning, during which time the gonads mature (Quinn 2005). Quinn (2005) classifies this type of migration as making 'the best of a bad situation'. It is well documented that fitness increases the longer an anadromous individual can remain in seawater and feed, prior to migrating for spawning (Leggett 1976). The theory for the early migration of some fish species like Chinook Salmon, is related to undertaking extensive migrations under limited time windows when river reaches are accessible, forcing immature individuals to migrate early and mature sexually while in freshwater (Quinn 2005). The sexual maturation of Broad Whitefish during the beginning portion of the spawning migration has not been documented, but the assumption that Broad Whitefish begin the spawning migration with under ripe gonads is probable and as the fish migrate, their gonads mature. Individuals caught in late summer have low GSI compared with individuals caught in late September and October (VanGerwen-Toyne *et al.* 2008). It should be noted that all fish captured in the Arctic Red River during the time of this study are assumed to be anadromous, although there

is speculation that riverine populations may exist in the Mackenzie River System, but to date there has been no published evidence. The presence of a riverine population may account for the large variability in the GSI values – possibly some riverine type Broad Whitefish could be involved. However, due to the clear pattern of increasing GSI over the fall, I can assume that any contribution by potential riverine Broad Whitefish to the data is minimal and does not affect the outcome of the results. The variation in timing of migration among all fish species relates to the fundamental constraint of spawning date and the problem of access to the spawning grounds (Quinn 2005).

#### *Migration Behaviour by Sex*

Migration behaviour between sexes of the same species can vary; however this is not a common trait, or at least not well documented (Karppinen *et al.* 2004). Female Broad Whitefish appear to migrate at a constant abundance over the entire time of spawning migration up the Arctic Red River (females are constantly trickling in), whereas, there is weak evidence suggesting that males may migrate in mass abundance. VanGerwen-Toyne *et al.* (2008) documented that in 2001 there was a large isolated peak of migrating male Broad Whitefish captured in the Peel River. It is assumed that this occurs annually; however, due to dangerous ice conditions on the river at the corresponding time this was not detected in other years of the study. Karppinen *et al.* (2004) also presents a sex-related difference in migration patterns suggesting that female Atlantic Salmon migrate up the River Tana in Finland, displaying more variable and stepwise migration patterns compared to their male counterparts. In Chum Salmon, males arrive before females on the spawning grounds (McKinstry 1993 *in* Quinn 2005). This is opposite to what is expected as the females are the nest builders not the males (Quinn 2005). Similarly Lake Cisco males have been documented to arrive on the spawning grounds days prior to the females (Scott and Crossman

1973). Lastly, Leggett (1976) noted that female American Shad ascending the Connecticut River entered later than the males and travelled at a faster daily rate (average female daily rate = 7.1 km/day; average male daily rate = 5.8 km/day). Sex migration differences are not considered a common occurrence but when present, the difference is biologically significant in the life history and migratory tendencies of the species as a whole. Further research on the differences in migration behaviour between male and female Broad Whitefish is needed. Restrictions on fishing during certain parts of the Broad Whitefish migration in the Arctic Red River may become important, particularly when large numbers of a single sex can be caught, altering the sex ratios and decreasing overall population fitness.

#### *Habitat Selection during Migration – Water Velocity*

Broad Whitefish in the Arctic Red River migrate when water velocity is slow throughout the water column (0.00 – 0.08 m/s). If Broad Whitefish were to migrate one month earlier they would face discharge levels up to 2.5 times higher (Appendix J). This leads to the idea that the specific time of migration in the Arctic Red River during the year (e.g. October not August), may be the way that Broad Whitefish ‘select’ low water velocity for migration.

Water velocity has been reported as being an important factor to other migrating species as it one of the primary factors affecting energy expenditure of the migrating fish (Yi *et al.* 2010, Quinn *et al.* 1997, Quinn 2005). Faster currents require a fish to expend more energy to swim against the water and move upstream compared to slower currents. Most notably research on Pacific salmon shows that as the salmon migrate up fast flowing rivers they select migration paths which increase energy efficiency by migrating along the bottom and the banks of the river where water velocity is slowest (Quinn 2005, Hinch and Rand 1998). Osborne (1961) found that as discharge in a river decreased the travel rate of Sockeye Salmon increased; leading Osborne (1961)

to propose that weaker currents might allow Sockeye Salmon to ascend the river faster. Quinn *et al.* (1997) found that as both water velocity and temperature decreased the energy expended by migrating salmon decreased. In addition to Pacific salmon, the spawning migration of Chinese Sturgeon (*Acipenser sinensis*) is heavily limited by water velocity (Yi *et al.* 2010). The Yangtze River where Chinese Sturgeon migrate to spawn in the fall is a wide and slow flowing river, allowing the fish to migrate at an energetically efficient pace to ensure successful spawning (Yi *et al.* 2010). Fast flowing water has negative impacts on the habitat available for Chinese Sturgeon spawning (Yi *et al.* 2010). Yi *et al.* (2010) determined that water discharge levels of 12,000 m<sup>3</sup>/s provided the sturgeon with the most abundance of spawning habitats within the river. In contrast when water discharge levels reached 20,000 m<sup>3</sup>/s or higher sturgeon spawning habitat availability decreased within the Yangtze River.

Similarly to Broad Whitefish, adult anadromous Masu Salmon begin migrating months prior to spawning. The Masu Salmon migrate upstream to holding pools where they wait for the correct time and conditions to complete their migration to the spawning grounds (Tago 2000 *in* Edo and Suzuki 2003). Masu Salmon select holding pools that are deep, that have cover and that have low water velocity. Selecting holding pools with slow water velocity allow Masu Salmon to conserve energy along their migration (Edo and Suzuki 2003). In contrast, Heggenes *et al.* (1996) found that habitat availability of juvenile Atlantic Salmon decreases with decreasing water velocity. This is because juvenile Atlantic Salmon are drift feeders who take advantage of increased abundance of prey with increasing water velocity. Habitat selection by drift feeding fish is strongly affected by current velocity, which involves a trade-off between energy expenditure and gain (Fausch 1993). However, Broad Whitefish like many anadromous migratory species do not feed while migrating and thus, can choose habitats with low water velocity as an energy saving strategy (Edo and Suzuki 2003).

### *Summary of Research Findings*

This research has added new knowledge about the habitat use of Broad Whitefish in the Mackenzie River system, in particular the Arctic Red River during Broad Whitefish spawning migrations. This research is the first to my knowledge that demonstrates empirical evidence of a spawning migration of Broad Whitefish in the Arctic Red River between mid-October and early November. It is now documented that Broad Whitefish are present in the Arctic Red River in large abundance in the fall for the purpose of spawning.

In addition, I developed a cumulative logit model from which maturity stage of Broad Whitefish can be predicted and characteristics of Broad Whitefish migrations revealed. For the first time evidence of a sex based difference in migration strategy is suggested. Female Broad Whitefish may be continuously migrating to the spawning grounds while male Broad Whitefish may arrive in a large congregation. This is a unique finding that was unexpected and requires further investigation.

Habitat selection within the water column during migration has never been studied in Broad Whitefish to my knowledge. I found that the water column in the Arctic Red River was very slow flowing at the time of Broad Whitefish migration and water velocity is not a barrier to fish migration. In contrast to other migrating fish species, I found that Broad Whitefish migrate in the middle of the water column instead of along the banks and bottom of the river. This is the first study to present a current profile for the Arctic Red River and the first study to look at Broad Whitefish location in the river column at the time of migration.

There has been research on the swimming performance of Broad Whitefish conducted in laboratory settings. This is the first research to my knowledge that tested Broad Whitefish swimming performance at the time of spawning migration in the field. From this research for the

first time a swim curve for Broad Whitefish has been developed and presented. Lastly, I presented evidence that the most efficient swimming speed for Broad Whitefish is 1.2 *L/s*. These findings are consistent with the optimal swimming speeds of other fish species. I only tested the prolonged swimming speeds of Broad Whitefish, more research is required to look at burst swim speeds using fixed velocity tests and critical swimming speeds using increasing velocity tests.



## *Conclusion*

Broad Whitefish is a fish species that is well adapted to the Arctic environment in which it persists. Broad Whitefish make long migrations to habitats that are optimal for spawning, at times that are most energetically efficient for the adults. Broad Whitefish have evolved to survive in the harsh Arctic environment of the Mackenzie River system and thrive. There are several aspects of ecology of Broad Whitefish that allow them to function well in the Arctic environment and differ from similar taxa (such as Pacific and Atlantic salmon) that live in north temperate environments. In contrast to Pacific and Atlantic salmon, Broad Whitefish appear to be able to migrate during a period of very cold temperatures. They migrate up large rivers when flows are near nil and thus do not require a high energy body type to effectively ascend the system. They are iteroparous animals in contrast to the semelparous life history of most Pacific salmon and thus put less energy into gonad production at each reproductive event. These findings support the view that Broad Whitefish conserve energy carefully during their reproductive period. They likely maintain a considerable reserve of energy for maintenance to survive for another day. This adaptation allows them to hedge their bets against the extremely unpredictable environment of the Arctic.

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Appendix A. A description of the relative stages of maturity used for Broad Whitefish (Bond and Erickson 1985).

	Female		Male	
Maturity Stage	Code	Description	Code	Description
Immature (virgin)	F1	<ul style="list-style-type: none"> <li>- Ovaries granular in texture</li> <li>- Hard and triangular in shape</li> <li>- up to full length of body cavity</li> <li>- membrane firm</li> <li>eggs distinguishable</li> </ul>	M6	<ul style="list-style-type: none"> <li>- Testes long and granular</li> <li>- tubular and scalloped shape</li> <li>- up to full body length</li> <li>putty-like firmness</li> </ul>
Mature (spawner)	F2	<ul style="list-style-type: none"> <li>- Current year spawner</li> <li>- ovary fills body cavity</li> <li>- eggs near full size but not loose</li> <li>- not expelled by pressure</li> </ul>	M7	<ul style="list-style-type: none"> <li>- Current year spawner</li> <li>- testes large and lobate</li> <li>- white to purplish colour</li> <li>- centers may be fluid</li> <li>- milt not expelled by pressure</li> </ul>
Ripe	F3	<ul style="list-style-type: none"> <li>- Ovaries greatly extended and fill body cavity</li> <li>- eggs full size and transparent</li> <li>- eggs expelled by slight pressure</li> </ul>	M8	<ul style="list-style-type: none"> <li>- Testes full size</li> <li>- white and lobate</li> <li>- milt expelled by slight pressure</li> </ul>
Spent	F4	<ul style="list-style-type: none"> <li>- Spawning complete</li> <li>- ovaries ruptured and flaccid</li> <li>- seed eggs visible</li> <li>- some retained eggs in body cavity</li> </ul>	M9	<ul style="list-style-type: none"> <li>- Spawning complete</li> <li>- tests flaccid with some milt</li> <li>- blood vessels obvious</li> <li>- testes violet-pink in colour</li> </ul>
Resting	F5	<ul style="list-style-type: none"> <li>- Ovaries 40-50% of body cavity</li> <li>- membrane thin, loose and semi-transparent</li> <li>- healed from spawning</li> <li>- seed eggs apparent with few atretic eggs</li> <li>- some eggs may be retained in body cavity</li> </ul>	M10	<ul style="list-style-type: none"> <li>- Testes tubular, less lobate</li> <li>- healed from spawning</li> <li>- no fluid in center</li> <li>- usually full length</li> <li>- mottled and purplish in colour</li> </ul>
Unknown (virgin)	0	<ul style="list-style-type: none"> <li>- cannot be sexed</li> <li>- gonads long or short and thin</li> <li>- transparent or translucent</li> </ul>		

## Appendix B. Extra information on hydrodynamics of flowing water

### *Boundary Layer Concept:*

Prandtl (1904) divided the flow around objects into two regions. The boundary layer is the region of flow around an object, where the fluid velocity increases from the object to that of the undisturbed fluid of the outer flow (Webb 1975). The boundary layer is in contact with the body surface. Here, the velocity of the fluid varies from the surface to which it sticks to the velocity of the free stream (Webb 1975). This region is characterized by having a steep velocity gradient and by fluid subject to extensive distortion (Webb 1975). Within the boundary region, the viscous forces are large, while the inertial forces are small and insignificant (Webb 1975).

The second region, the outer flow region, is outside of the boundary layer. Here, inertial forces are large and significant, while the viscous forces are insignificant or nonexistent (Webb 1975).

The boundary layer region and the outer flow region can greatly affect one another. Conditions in the outer flow region can cause the boundary layer to separate from the surface, producing trailing vortices and increasing the wake (Webb 1975). When the boundary layer separates, it affects the outer flow region and, consequentially, drag (Webb 1975).

The thickness of the boundary layer is distinct to each object under each situation. There are two ways to define this thickness. First, the velocity thickness is defined as the distance from the surface to the position where the velocity of the fluid differs by 1% from the free stream velocity (Webb 1975). Second, the displacement thickness defined as the distance from the surface by which the streamlines of the outer flow are displaced by the boundary layer (Webb 1975). The thickness of the boundary layer is determined by surface area – fluid interactions, surface roughness, character of free stream flow, pressure and free stream velocity. The surface area - fluid interactions affect the boundary layer thickness over the surface of the object. The

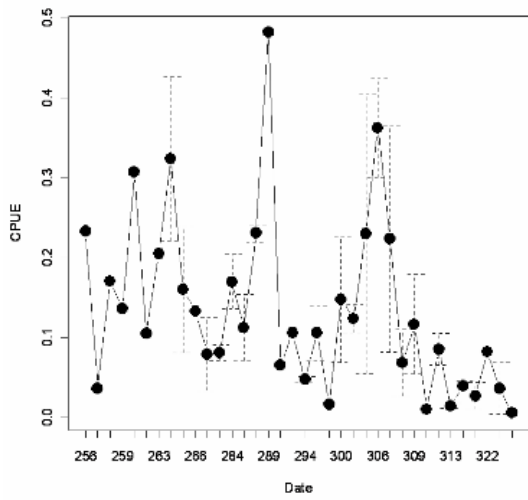
boundary layer is thinnest at the front end of the object (e.g. snout of the fish) and the thickness increases posterior, or downstream, over the object because more free stream fluid is being affected (Webb 1975).

The roughness of the surface of the object does not affect the boundary layer thickness, but rather encourages the transition between laminar and turbulent boundary layer flow. This adaptation is most effective at low speeds (Webb 1975).

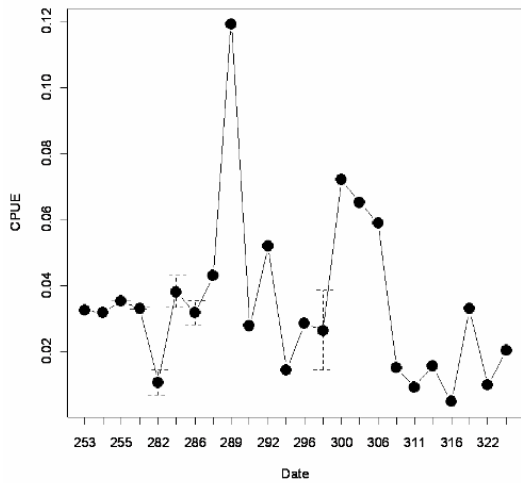
Stream flow (laminar or turbulent) largely affects the thickness of the boundary layer. Turbulent free stream flow encourages turbulent boundary layer flow (Webb 1975), resulting in a thicker boundary layer (Hynes 1972). The pressure of the aquatic system affects boundary layer thickness. High pressure in the outer flow regions impresses on the boundary layer, decreasing thickness and increasing boundary layer flow (Webb 1975).

Free stream velocity also influences boundary layer thickness. Faster-flowing water decreases the thickness of the boundary layer (Hynes 1972).

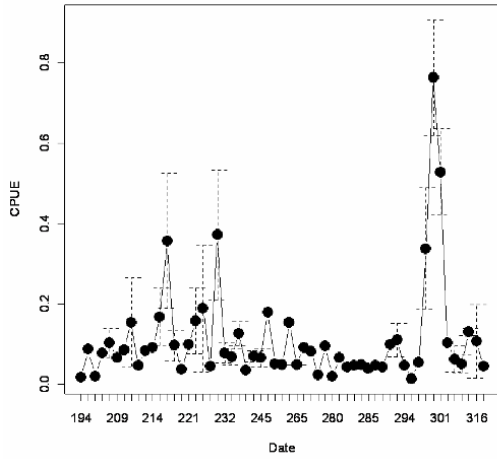
Appendix C: CPUE graphs for 1992 and 1992 with different nets.



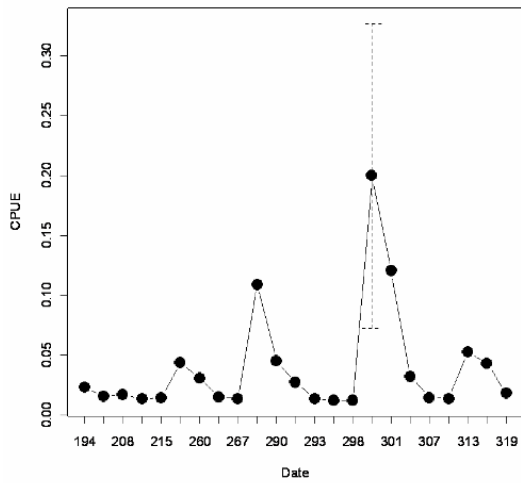
Plot of Means CPUE for 1992 commercial nets (5.5 Mesh)



Plot of Means for 1992 CPUE, experimental nets (varying mesh sizes, most common 4 inch).



Plot of Means for 1993 CPUE commercial nets (mesh 5.5 inch). Standardized for net length (25 m) and net height (1.83 m), standard error bars included.



Plot of Means for 1993 CPUE experimental nets (varying mesh sizes most common mesh 4.0 inch). Standardized for net length (25 m) and net height (1.83 m), standard error bars included.

## Appendix D: Piecewise Regression Information and R Coding

Piecewise regression is a regression that fits different functions over different ranges of the explanatory variable (Neter *et al.* 1990b). The simplest example is different regression lines may be fit to the left-hand side and the right-hand side of a scatterplot (Crawley 2007). The piecewise regression is:

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 (X_{i1} - t) X_{i2} + \epsilon_i$$

where,  $Y_i$  is the response variable,  $\beta_0$  and  $\beta_1 + \beta_2$  are the slopes,  $X_{i1}$  is the predictor variable,  $X_{i2}$  is the dummy variable (1 if  $X_{i1} > K$ , 0 if otherwise) (Neter *et al.* 1990a)

R coding for Piecewise Regression example used: 1993 CPUE data.

### **#Graph of the data**

```
plot(CPUE.net.height.correction~JDAY,pch=16)
```

### **#Model to calculate residuals, plot of the residuals predicted from model 1**

```
model1<-lm((CPUE.net.height.correction)~(JDAY))  
plot((JDAY),resid(model1))
```

### **#Model that incorporates a random break point in the piecewise regression**

```
model2<-lm((CPUE.net.height.correction)~(JDAY)*(JDAY<300)+(JDAY)*(JDAY>=300))
```

### **#Sorts the data, cleans up output**

```
sort(unique(JDAY))
```

### **# Loop of the data (9 times) that displays an index graph from which break points can be #drawn**

```
Break<-sort(unique(JDAY))  
d<-numeric(9)  
for(i in 1:41)  
+ {model<-  
lm((CPUE.net.height.correction)~(JDAY<Break[i])*(JDAY)+(JDAY>=Break[i])*(JDAY))  
+ d[i]<-summary(model)[[6]]}  
plot(d,type="l")
```

**#Break points read off index graph (see above)**

```
Break[30]
```

```
Break[19]
```

```
Break[22]
```

**#Piecewise regression with 1 break point determined from index graph**

```
model2<-lm((CPUE.net.height.correction)~(JDAY<306)*(JDAY)+(JDAY>=306)*(JDAY))
```

**#Plot of the data with the piecewise regression line from model 2 included**

```
area=sort(unique(JDAY))
```

```
plot(CPUE.net.height.correction~JDAY,xlab="Date",ylab="CPUE",pch=16)
```

```
lines((area),predict(model2,list(JDAY=area)))
```

**#Piecewise regression with 2 break points determined from the index graph**

```
model3<-
```

```
lm((CPUE.net.height.correction)~(JDAY<292)*(JDAY)+(JDAY>=292&JDAY<306)*(JDAY)+(JDAY>=306)*(JDAY))
```

**#Plot of the data with the piecewise regression line from model 3 included**

```
area=sort(unique(JDAY))
```

```
plot(CPUE.net.height.correction~JDAY,xlab="Date",ylab="CPUE",pch=16)
```

```
lines((area),predict(model3,list(JDAY=area)))
```

**#Piecewise regression with 3 break points determined from the index graph**

```
model4<-
```

```
lm((CPUE.net.height.correction)~(JDAY<288)*(JDAY)+(JDAY>=288&JDAY<292)*(JDAY)+(JDAY>=292&JDAY<306)*(JDAY)+(JDAY>=306)*(JDAY))
```

```
area=sort(unique(JDAY))
```

```
plot(CPUE.net.height.correction~JDAY,xlab="Date",ylab="CPUE",pch=16)
```

```
lines(area,predict(model4,list(JDAY=area)))
```



## Appendix E: Akaike's Information Criterion (AIC) Information and R Coding

Akaike's Information Criterion (AIC) is a theoretical basis for model selection (Anderson 2008) based on an optimization criterion (Hilborn and Mangel 1997). The AIC model is:

$$\text{AIC} = G^2 - n + 2p$$

where,  $G^2$  is the deviance for a given model,  $n$  is the number of observations and  $p$  is the predictor variables (parameters) (Quinn and Keough 2002). The AIC 'penalizes' the goodness of fit of the model for every free parameter by adding 2 to the negative log likelihood (Hilborn and Mangel 1997). In AIC is performed for every model in the set (Anderson 2008) and the model with the lowest AIC is selected (Hilborn and Mangel 1997). This selection process chooses the model that minimizes the information lost when approximating full reality by a fitted model (Anderson 2008).

R coding for AIC example used: 1993 CPUE data.

**#AIC for model 2, model 3 and model 4 from piecewise regression**

```
AIC(model2,model3,model4)
```

## Appendix F: R Coding used for non-parametric smooth curves

```
attach(nonparametric_93)
names(nonparametric_93)
```

### *Loess Smooth Curve Model:*

```
par(mfrow=c(2,2))
plot(JDAY,CPUE.corrected.nd,pch=16,xlab="Date",ylab="CPUE")
text(240,2.5,"loess",pos=2)
model<-loess(CPUE.corrected.nd~JDAY)
xv<-190:322
yv<-predict(model,data.frame(JDAY=xv))
lines(xv,yv)
```

### *Gam Smooth Curve Model:*

```
plot(JDAY,CPUE.corrected.nd,pch=16,xlab="Date",ylab="CPUE")
text(240,2.5,"gam",pos=2)
library(mgcv)
model<-gam(CPUE.corrected.nd~s(JDAY))
yv<-predict(model,list(JDAY=xv))
lines(xv,yv)
```

### *Polynomial Smooth Curve Model:*

```
plot(JDAY,CPUE.corrected.nd,pch=16,xlab="Date",ylab="CPUE")
text(250,2.5,"polynomial",pos=2)
model<-lm(CPUE.corrected.nd~JDAY+I(JDAY^2)+I(JDAY^3))
yv<-predict(model,list(JDAY=xv))
lines(xv,yv)
```

## Appendix G: Cumulative Logit Model Information

A cumulative logit model is a generalized logistic regression model that handles multicategory response variable which is ordinal and explanatory variables which can be continuous or categorical (Agresti 1996). This model treats one variable as a response and the other(s) as explanatory. It is assumed that the response counts at each combination have a multinomial distribution and that multinomial counts at different combinations are independent (Agresti 1990). In this model the response categories are ordered so logits can directly incorporate the ordering (Agresti 1996). A logit is a link function between the random and systematic components. A link function specifies how  $\mu = E(Y)$  relates to the explanatory variables in the linear predictor. The link function called logit,

$$\text{logit} [ P(Y \leq j) ] = \log [ P(Y \leq j) / 1 - P(Y \leq j) ] \quad (1)$$

models the log odds. Logit links are used when  $\mu$  is between 0 and 1, such as with probabilities (Agresti 1996).

Cumulative logit models are based on cumulative probabilities (Bender and Benner 2000). Cumulative probabilities are the probabilities that the response  $Y$  falls in category  $j$  or below, for each possible  $j$ . The  $j$ th cumulative probability is:

$$P(Y \leq j) = \pi_1 + \dots + \pi_j, \quad j = 1, \dots, J \quad (\text{Agresti 1996}) \quad (2)$$

Cumulative logit models are based on the view that  $Y$  is a mathematically discrete variable of an underlying continuous trait defined by cut-off points  $j$  (Bender and Benner 2000). The

standard assumption in most applications is that the regression coefficient does not depend on  $j$ , so the cumulative model is:

$$\text{logit} [ P(Y \leq j | x) ] = \alpha_j + \beta x, \quad j = 1, \dots, J-1 \quad (3)$$

where  $j$  = cut-off points,  $\alpha_j$  = cut point for the model and  $\beta$  is the effect parameter of  $x$ . A final assumption of the model is that each response category has equal slopes (Agresti 1990).

Finally, if the logit link function (1) is used in the cumulative model (3) the model becomes:

$$[P(Y \leq j | x)] = \exp(\alpha_j + \beta x) / [1 + \exp(\alpha_j + \beta x)] \quad (\text{Agresti 1990}) \quad (4).$$

## Appendix H: Cumulative Logit Model SAS Coding

SAS coding for the cumulative logit model:

*MALES*

*Imports your data file*

```
PROC IMPORT OUT= WORK.mat_1993
    DATAFILE= "H:\Master's Files\DATA 1992-1993\Maturity
Model\Maturity_Model_93_Oct_CD_SAS.xls"
    DBMS=EXCEL REPLACE;
    SHEET="mat_1993";
    GETNAMES=YES;
    MIXED=yes;
    SCANTEXT=YES;
    USEDATE=YES;
    SCANTIME=YES;
RUN;
```

```
proc print data= work.mat_1993;
```

*Remove Females and combines necessary Maturity Stages*

```
data three;
set work.mat_1993;
if sex = 'F' then delete;
if matstage = "M6" or matstage = "M7" then matstage = "M6.7";
if matstage = "M9" or matstage = "M10" then matstage = "M9+";
keep matstag matstage gsi cpue JDAY;
run;
```

```
PROC SORT DATA = THREE;BY MATSTAGE;
```

```
proc print data=three;
    var matstage gsi cpue jday;
run;
```

*Plots your data to see what it looks like*

```
proc plot data=three;
    plot matstage*gsi;
    plot matstage*cpue;
    plot matstage*jday;
run;
```

*Logistic Model (FULL) #1*

```
proc logistic data=three;

    Class MATSTAG/order=data param=reference reference=first;
    model matstage(reference='M6.7')=GSI Cpue JDAY/ link=glogit scale = none
aggregate lackfit;
    output out=MyData predprobs = individual;
run;
```

*Creates an output of the logistic model results*

```
options orientation=landscape;
ods pdf file = "Male.AIC.1_1.pdf";
proc print data= mydata;
```

```

        title2 'output from Model M_1';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;
proc logistic data=three;

Logistic Model #2
    Class MATSTAG/order=data param=reference reference=first;
    model matstage(reference='M6.7')=GSI Cpue/ link=glogit scale = none
aggregate lackfit;
    output out=MyData predprobs = individual;
    run;
options orientation=landscape;
ods pdf file = "Male.AIC.1_2.pdf";
proc print data= mydata;

        title2 'output from Model M_2';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;

proc logistic data=three;

Logistic Model #3
    Class MATSTAG/order=data param=reference reference=first;
    model matstage(reference='M6.7')=GSI JDAY/ link=glogit scale = none
aggregate lackfit;
    output out=MyData predprobs = individual;
    run;
options orientation=landscape;
ods pdf file = "Male.AIC.1_3.pdf";
proc print data= mydata;

        title2 'output from Model M_3';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;
proc logistic data=three;

Logistic Model #4
    Class MATSTAG/order=data param=reference reference=first;
    model matstage(reference='M6.7')=GSI/ link=glogit scale = none aggregate
lackfit;
    output out=MyData predprobs = individual;
    run;
options orientation=landscape;
ods pdf file = "Male.AIC.1_4.pdf";
proc print data= mydata;

        title2 'output from Model M_4';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;

```

```

proc logistic data=three;

Logistic Model #5
  Class MATSTAG/order=data param=reference reference=first;
  model matstage(reference='M6.7')=Cpue JDAY/ link=glogit scale = none
aggregate lackfit;
  output out=MyData predprobs = individual;
  run;
options orientation=landscape;
ods pdf file = "Male.AIC.1_5.pdf";
proc print data= mydata;

      title2 'output from Model M_5';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;
proc logistic data=three;

Logistic Model #6
  Class MATSTAG/order=data param=reference reference=first;
  model matstage(reference='M6.7')= Cpue/ link=glogit scale = none
aggregate lackfit;
  output out=MyData predprobs = individual;
  run;
options orientation=landscape;
ods pdf file = "Male.AIC.1_6.pdf";
proc print data= mydata;

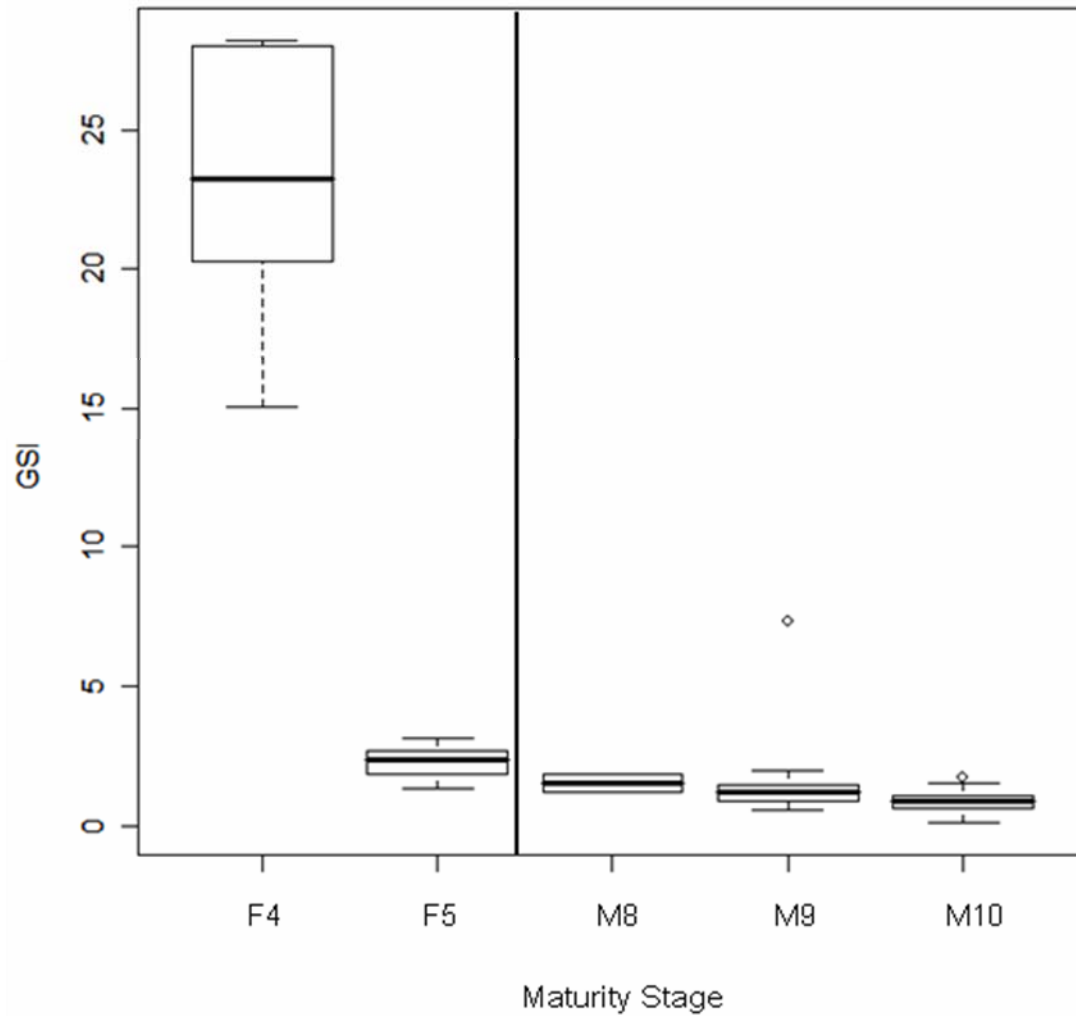
      title2 'output from Model M_6';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;
proc logistic data=three;

Logistic Model #7
  Class MATSTAG/order=data param=reference reference=first;
  model matstage(reference='M6.7')= JDAY/ link=glogit scale = none
aggregate lackfit;
  output out=MyData predprobs = individual;
  run;
options orientation=landscape;
ods pdf file = "Male.AIC.1_7.pdf";
proc print data= mydata;

      title2 'output from Model M_7';
run;
ods pdf close;
ods pdf(id=d3dstyle) close;
run;
quit;

```

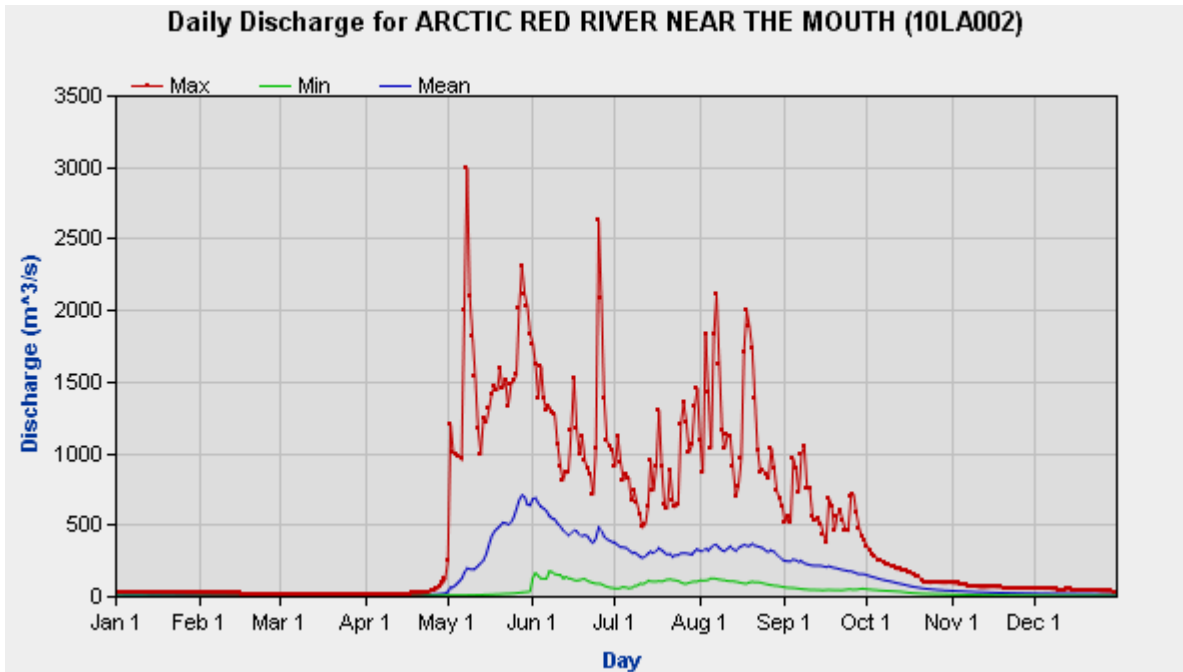
Appendix I: Maturity Stages compared to GSI for 1992 data.



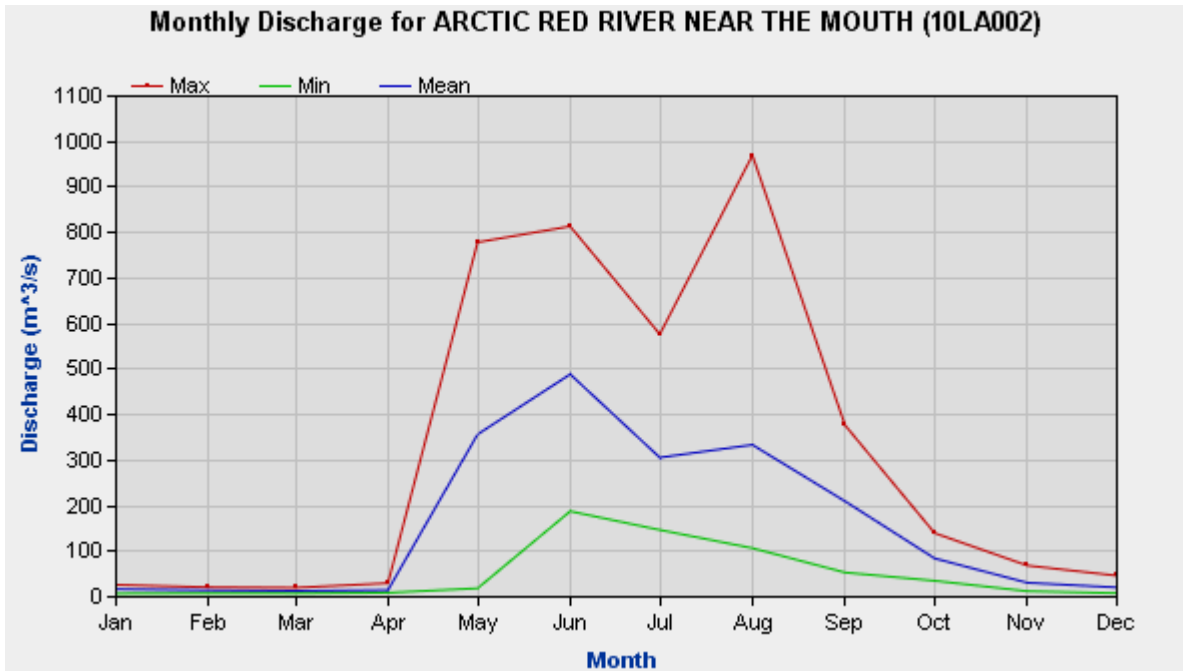
The GSI related to maturity stage for broad whitefish captured in 1992. Coding for the maturity stage F4: Female Spent, F5: Female Resting, M8: Male Ripe, M9: Male Spent, M10: Male Resting (Appendix A).



Appendix J: Graphs of the Arctic Red River measured discharge annually.



[http://www.wsc.ec.gc.ca/staflo/index\\_e.cfm?cname=flow\\_daily.cfm&first=1968&last=2009](http://www.wsc.ec.gc.ca/staflo/index_e.cfm?cname=flow_daily.cfm&first=1968&last=2009)  
Daily water discharge



[http://www.wsc.ec.gc.ca/staflo/index\\_e.cfm?cname=flow\\_monthly.cfm&first=1968&last=2009](http://www.wsc.ec.gc.ca/staflo/index_e.cfm?cname=flow_monthly.cfm&first=1968&last=2009)  
Monthly discharge ARR near mouth

Appendix K: Swimming performance data of Broad Whitefish from the Arctic Red River at the time of their spawning migration.

<b>Date</b>	<b>Fork Length (mm)</b>	<b>Weight (g)</b>	<b>Water Velocity (m/s)</b>	<b>Exhaustion Time (mins)</b>
Nov 9	530	2365	0.345	120
Nov 8	486	1512	0.345	31
Nov 8	458	1188	0.345	59
Oct 22	461	1553	0.425	120
Oct 23	446	1051	0.425	39.62
Nov 8	491	1607	0.425	50.75
Nov 8	493	1416	0.425	120
Oct 23	512	2030	0.515	32.08
Oct 24	479	1545	0.555	40.17
Nov 7	510	2352	0.555	69
Nov 8	475	1566	0.555	120
Oct 24	531	1961	0.67	120
Nov 8	545	2156	0.67	95.17
Nov 10			0.67	84
Oct 25	565	2669	0.775	9
Nov 7	470	1623	0.775	78.5
Nov 8	485	1678	0.775	120
Oct 25	811	1747	0.845	33.17
Nov 8	476	1640	0.845	31
Nov 10	534	1725	0.845	120
Nov 7	518	2151	0.93	29
Nov 9	435	1123	0.93	5.67
Nov 6	497	1880	1.045	12.55
Nov 9	520	2303	1.045	21
Nov 6	506	1672	1.105	11
Nov 6	518	2136	1.105	37.17
Nov 9	460	1189	1.105	10
Nov 6	527	1837	1.265	55.33
Nov 6	495	1571	1.265	8
Nov 6	509	1890	1.305	30.5

APPENDIX L: Generalized Linear Model applied to male and female Broad Whitefish migrations in the Arctic Red River in 1993.

***Quasi Binomial Males***

Whole data set

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM1)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.120951	-0.028327	-0.002606	0.021578	0.111820

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-3.774309	0.346734	-10.885	<2e-16 ***
Cpue	-0.034812	0.045231	-0.770	0.4428
date	-0.002161	0.001205	-1.793	0.0751 .

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.001579705)

Null deviance: 0.23163 on 144 degrees of freedom

Residual deviance: 0.22419 on 142 degrees of freedom

Number of Fisher Scoring iterations: 7

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM1)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.83890	0.02481	0.13245	0.19320	0.66642

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-3.78568	3.20196	-1.182	0.2391
Cpue	2.83652	2.65361	1.069	0.2869
date	0.02389	0.01201	1.990	0.0486 *

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.558266)

Null deviance: 29.206 on 144 degrees of freedom

Residual deviance: 23.650 on 142 degrees of freedom

Number of Fisher Scoring iterations: 9

July to Sept 5

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM2)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.048979	-0.020237	-0.003851	0.007536	0.078104

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-5.975352	1.596067	-3.744	0.0028 **
Cpue	0.062024	0.658679	0.094	0.9265
date	0.006978	0.006745	1.035	0.3213

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.001407339)

Null deviance: 0.017356 on 14 degrees of freedom

Residual deviance: 0.015785 on 12 degrees of freedom

Number of Fisher Scoring iterations: 7

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM2)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.9878	0.4043	0.5357	0.5998	0.6583

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	8.16840	16.85002	0.485	0.637
Cpue	-0.02575	6.46555	-0.004	0.997
date	-0.02720	0.07047	-0.386	0.706

(Dispersion parameter for quasibinomial family taken to be 1.188736)

Null deviance: 11.780 on 14 degrees of freedom

Residual deviance: 11.572 on 12 degrees of freedom

Number of Fisher Scoring iterations: 5

Sept 20<sup>st</sup> to October 21

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM3)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.073806	-0.029021	-0.009731	0.028304	0.070916

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-4.0961470	2.3107982	-1.773	0.0966 .
Cpue	-3.0367747	1.4933114	-2.034	0.0601 .
date	0.0003811	0.0081781	0.047	0.9635

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.001926291)

Null deviance: 0.037505 on 17 degrees of freedom

Residual deviance: 0.028369 on 15 degrees of freedom

Number of Fisher Scoring iterations: 7

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM3)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.3367	0.3462	0.4512	0.5754	0.9302

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-17.68966	0.01429	-0.884	0.391
Cpue	-2.46175	12.96059	-0.190	0.852
date	0.07050	0.07268	0.970	0.347

(Dispersion parameter for quasibinomial family taken to be 1.393754)

Null deviance: 16.220 on 17 degrees of freedom

Residual deviance: 14.686 on 15 degrees of freedom

Number of Fisher Scoring iterations: 5

Oct 29 to Nov 12

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM4)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.111031	-0.027795	-0.002689	0.021517	0.085323

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	6.608381	2.706850	2.441	0.01624 *
Cpue	-0.215024	0.071316	-3.015	0.00320 **
date	-0.035655	0.008701	-4.098	8.05e-05 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.001294734)

Null deviance: 0.16314 on 111 degrees of freedom

Residual deviance: 0.14159 on 109 degrees of freedom

Number of Fisher Scoring iterations: 7

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM4)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.480e+00	4.915e-07	7.885e-07	1.023e-01	4.874e-01

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	67.0233	43.0433	1.557	0.1223
Cpue	15.6510	8.5793	1.824	0.0708 .
date	-0.2101	0.1384	-1.518	0.1320

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.1987374)

Null deviance: 11.4280 on 111 degrees of freedom

Residual deviance: 8.1195 on 109 degrees of freedom

Number of Fisher Scoring iterations: 12

BEFORE Oct 30<sup>th</sup>

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM5)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.074634	-0.027133	-0.002378	0.018842	0.096210

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-4.895436	0.421289	-11.620	< 2e-16 ***
Cpue	-0.195308	0.057402	-3.402	0.000968 ***
date	0.002462	0.001588	1.550	0.124349

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.001219862)

Null deviance: 0.13054 on 100 degrees of freedom

Residual deviance: 0.11585 on 98 degrees of freedom

Number of Fisher Scoring iterations: 7

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM5)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.24960	0.02740	0.02898	0.15075	0.75586

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-7.59730	3.31909	-2.289	0.02423 *
Cpue	1.86104	1.84322	1.010	0.31514
date	0.04119	0.01408	2.925	0.00428 **

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.2434605)

Null deviance: 19.648 on 100 degrees of freedom

Residual deviance: 13.805 on 98 degrees of freedom

Number of Fisher Scoring iterations: 10

AFTER Oct 30th

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM6)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.115918	-0.030133	-0.005894	0.023644	0.076701

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	4.63105	5.63375	0.822	0.416
Cpue	-0.77639	0.63522	-1.222	0.229
date	-0.02894	0.01828	-1.583	0.121

(Dispersion parameter for quasibinomial family taken to be 0.001816638)

Null deviance: 0.091509 on 43 degrees of freedom

Residual deviance: 0.076985 on 41 degrees of freedom

Number of Fisher Scoring iterations: 7

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMM6)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.47978	0.04645	0.10240	0.23578	0.48730

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	66.986	70.250	0.954	0.346
Cpue	15.640	14.014	1.116	0.271
date	-0.210	0.226	-0.929	0.358

(Dispersion parameter for quasibinomial family taken to be 0.52832)

Null deviance: 9.5455 on 43 degrees of freedom

Residual deviance: 8.1194 on 41 degrees of freedom

Number of Fisher Scoring iterations: 8



Quasi Binomial GLM Females

*All data*

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF1)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.463813	-0.203019	-0.005012	0.150710	0.451915

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-1.736635	0.619765	-2.802	0.007035 **
Cpue	-2.452027	0.679976	-3.606	0.000679 ***
date	0.001391	0.002229	0.624	0.535114

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.05316019)

Null deviance: 3.8813 on 56 degrees of freedom

Residual deviance: 3.0409 on 54 degrees of freedom

Number of Fisher Scoring iterations: 5

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF1)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7160	-0.5294	0.2459	0.4161	2.2898

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-12.12398	3.26321	-3.715	0.000483 ***
Cpue	-3.38422	3.07196	-1.102	0.275501
date	0.05038	0.01235	4.079	0.000150 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 1.059304)

Null deviance: 78.861 on 56 degrees of freedom

Residual deviance: 41.176 on 54 degrees of freedom

Number of Fisher Scoring iterations: 5

July to Sept 5<sup>th</sup>

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF2)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.2437322	-0.0644450	0.0006115	0.0447697	0.1901925

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-8.721408	0.916454	-9.516	5.89e-10 ***
Cpue	0.150374	0.304351	0.494	0.625
date	0.029300	0.003982	7.357	8.20e-08 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.007792254)

Null deviance: 0.65362 on 28 degrees of freedom

Residual deviance: 0.20490 on 26 degrees of freedom

Number of Fisher Scoring iterations: 5

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF2)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.9219	-0.4579	-0.2379	-0.1463	2.2541

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	22.31844	14.09971	1.583	0.126
Cpue	-1.70966	6.47881	-0.264	0.794
date	-0.10975	0.07023	-1.563	0.130

(Dispersion parameter for quasibinomial family taken to be 0.9537357)

Null deviance: 23.269 on 28 degrees of freedom

Residual deviance: 16.715 on 26 degrees of freedom

Number of Fisher Scoring iterations: 6

Sept 20<sup>th</sup> to Oct 21st

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF3)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.20498	-0.04367	0.02337	0.05927	0.12547

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-2.700070	1.752835	-1.540	0.158
Cpue	1.261429	1.578958	0.799	0.445
date	0.005567	0.006362	0.875	0.404

(Dispersion parameter for quasibinomial family taken to be 0.01098728)

Null deviance: 0.12179 on 11 degrees of freedom

Residual deviance: 0.10236 on 9 degrees of freedom

Number of Fisher Scoring iterations: 4

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF3)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.52085	0.06179	0.15492	0.38423	1.20017

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-55.1090	42.4054	-1.300	0.226
Cpue	-0.2452	21.7843	-0.011	0.991
date	0.2093	0.1598	1.310	0.222

(Dispersion parameter for quasibinomial family taken to be 0.6407312)

Null deviance: 10.8135 on 11 degrees of freedom

Residual deviance: 7.3427 on 9 degrees of freedom

Number of Fisher Scoring iterations: 7

*Nov 3<sup>rd</sup> to Nov 15<sup>th</sup>*

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF4)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.3454	-0.1911	-0.0893	0.1010	0.5218

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-20.42214	32.64819	-0.626	0.542
Cpue	-4.48090	2.24135	-1.999	0.067 .
date	0.06053	0.10310	0.587	0.567

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.07654114)

Null deviance: 1.3395 on 15 degrees of freedom

Residual deviance: 0.8397 on 13 degrees of freedom

Number of Fisher Scoring iterations: 6

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF4)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.8981	-0.9417	0.6173	0.7897	1.2384

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	21.59268	82.59629	0.261	0.798
Cpue	5.64936	5.73039	0.986	0.342
date	-0.07043	0.26157	-0.269	0.792

(Dispersion parameter for quasibinomial family taken to be 1.305982)

Null deviance: 19.875 on 15 degrees of freedom

Residual deviance: 18.031 on 13 degrees of freedom

Number of Fisher Scoring iterations: 4

BEFORE Oct 30<sup>th</sup>

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF5)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.227500	-0.058198	-0.001393	0.043211	0.264230

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-6.583406	0.506504	-12.998	1.46e-15 ***
Cpue	0.193350	0.328615	0.588	0.56
date	0.019788	0.001877	10.541	7.75e-13 ***

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.01068280)

Null deviance: 2.04966 on 40 degrees of freedom

Residual deviance: 0.40852 on 38 degrees of freedom

Number of Fisher Scoring iterations: 5

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF5)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.6473	-0.6875	-0.3880	0.6635	2.3990

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-5.18346	4.63510	-1.118	0.270
Cpue	-8.53187	5.52847	-1.543	0.131
date	0.02448	0.01715	1.427	0.162

(Dispersion parameter for quasibinomial family taken to be 1.145987)

Null deviance: 52.644 on 40 degrees of freedom

Residual deviance: 36.702 on 38 degrees of freedom

Number of Fisher Scoring iterations: 5

AFTER Oct 30<sup>th</sup>

**glm(formula = GSI ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF6)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-0.3454	-0.1911	-0.0893	0.1010	0.5218

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-20.42214	32.64819	-0.626	0.542
Cpue	-4.48090	2.24135	-1.999	0.067
date	0.06053	0.10310	0.587	0.567

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Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasibinomial family taken to be 0.07654114)

Null deviance: 1.3395 on 15 degrees of freedom

Residual deviance: 0.8397 on 13 degrees of freedom

Number of Fisher Scoring iterations: 6

**glm(formula = MATSTAGE ~ Cpue + date, family = quasibinomial(logit),  
data = GLMF6)**

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.8981	-0.9417	0.6173	0.7897	1.2384

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	21.59268	82.59629	0.261	0.798
Cpue	5.64936	5.73039	0.986	0.342
date	-0.07043	0.26157	-0.269	0.792

(Dispersion parameter for quasibinomial family taken to be 1.305982)

Null deviance: 19.875 on 15 degrees of freedom

Residual deviance: 18.031 on 13 degrees of freedom

Number of Fisher Scoring iterations: 4