The migration, survival and movements of Atlantic salmon (*Salmo salar*) kelts originating from the Miramichi River system, NB.

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ABSTRACT

This thesis examines the migration and survival of Miramichi River Atlantic salmon kelts within the Miramichi estuary and Atlantic Ocean, with the goals of documenting their migratory characteristics, survival and possible long term effects of catch-and-release angling. A total of 100 kelts were tagged with acoustic telemetry tags in 2008 and 2009 (50 per year) and were passively tracked through the Miramichi estuary system and Atlantic Ocean. Kelt survival to the estuary exit was high; 96 % in 2008, 92 % in 2009 and 94 % combined. Of the kelts that survived, 11 returned as repeat spawners (seven consecutives, four alternates). They did not use the estuary as an overwintering ground after spawning. Kelts spent significantly different amounts of time in the upper, middle and lower reaches of the estuary during their exit and return. Once released, the majority of kelts spent more time between their release site and the first receiver downstream then in the remaining downstream sections of the estuary. Average speeds of travel were variable, differing between years, but speed increased as kelts progressed towards the estuary exit. Kelts entered the sea a short time after release (< 20 d). Once out of the Miramichi system, kelts were occasionally detected along the coast when leaving from and returning to the river system. Some kelts exited the Gulf of St. Lawrence via the Strait of Belle Isle (22 in 2008, 9 in 2009), over a period of 20 d in 2008 and 35 d in 2009. Speeds of travel for kelts within the Gulf of St. Lawrence varied from 10.4 km/d to 69.9 km/d. Repeat spawners that returned as consecutives in 2008 and 2009 did so between 44 and 64.8 d post sea entry. Alternates returned an average of 394.7 d post sea entry. Early stages of estuarine migration are important for early marine survival and the return of repeat spawners. Consecutive spawners may exit the Gulf to recondition. This research gives insight into the role that the early stage of estuary migration has upon the early survival and return of repeat spawners as well as into the migratory routes used and possible destinations for ocean bound kelts.

RÉSUMÉ

Cette thèse couvre la migration et la survie des saumons noir de l’Atlantique provenant de la Rivière Miramichi dans l’estuaire et dans l’océan Atlantique. Le but de cette thèse est de documenté leurs caractéristiques migratoire, leur survie et les effets possible de la graciation. Un total de 100 saumons noir ont été bagués en 2008 et en 2009 (50 par année) à l’aide de bagues de télémétrie acoustiques. Ceux-ci ont été suivis dans l’estuaire de la Rivière Miramichi et dans l’océan Atlantique. Leur survie jusqu'à la sortie de l’estuaire fut élevée (96 % en 2008, 92 % en 2009 et 94 % combiné). Des saumons qui ont survécut, 11 sont revenus afin de frayer de nouveau (sept consécutivement, quatre alternativement). Ils ne sont pas restés dans l’estuaire durant l’hiver après la fraie. Les saumons noir sont restés pour une période de temps différente dans les trois sections de l’estuaire (début, milieu, fin) durant la sortie et l’entrée. Après leur remise à l’eau, la plupart des saumons noir sont restés entre leur site de relâche et le premier receveur en aval. La vitesse de déplacement a augmenté dans chaque section, de l’endroit de relâche à la sortie de l’estuaire. La sortie de l’estuaire et l’entrée dans l’océan s’est faite en peu de temps (<20 jours). Dans le Golfe du St. Laurent, les saumons noir ont été documentés près des côtes. Ils sont sortis du Golfe du St. Laurent via le Détroit de Belle Isle (22 en 2008, 9 en 2009) se concentrant durant une période de 20 jours en 2008 et 35 jours en 2009. Dans le Golfe du St. Laurent la vitesse de déplacement se situait entre 10.4 km/jour et 69.9 km/jour. Les saumons sont retournés dans l’estuaire la même année entre 44 et 64.8 jours après leur sortie de l’estuaire, ou l’année suivante dans une moyenne de 394.7 jours après leur sortie de l’estuaire. Le début de leur migration dans l’estuaire peut être important pour leur survie dans l’océan et leur retour pour une autre fraie. Il est aussi possible que les saumons qui frayent chaque année sortent du Golfe afin d’acquérir l’énergie requise pour frayer. Cette recherche nous donne un aperçu du rôle que leur migration dans l’estuaire à sur leur survie immédiate et sur le retour des frayeurs. Cette recherche nous donne aussi un aperçu des routes de migration utilisées et des destinations possible des saumons dans l’océan Atlantique.

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PREFACE

This thesis is manuscript-based and consists of three chapters. Each has its own literature cited section. Chapters two and three share the appendices section at the end of the thesis. The first chapter is a literature review and overall introduction (Chapter 1: Literature review and general introduction). The second chapter follows the style of the Canadian Journal of Fisheries and Aquatic Science where it is planned to be submitted. This chapter examines the migration and survival of kelts as they exit the Miramichi estuary and discusses the importance of this migratory stage to their overall survival (Chapter 2: The estuarine movements and survival-to-return of Atlantic salmon kelts from the Miramichi River system, NB). The third chapter (Chapter 3: The migratory movements of Miramichi Atlantic salmon kelts within the Gulf of St. Lawrence and Atlantic ocean coastline) follows the style of the Journal of Fish Biology where it is planned to be submitted. This chapter examines the kelts migratory progression along the Atlantic Ocean coastline through the Gulf of St. Lawrence once they have left the Miramichi system, and infers the migratory pathways different age classes of kelts may take.

CONTRIBUTION OF AUTHORS

The candidate is the primary author for chapters two and three. I was responsible for organizing, planning, implementing and executing the field research. I also collected, compiled and analyzed the data and wrote the two manuscripts. F. G. Whoriskey and M. Curtis are junior authors for chapters two and three. They helped in the organization and planning of the study and aided with analytical and editorial guidance for the manuscripts.

CHAPTER 1: LITERATURE REVIEW AND GENERAL INTRODUCTION

Distribution

The Atlantic salmon (*Salmo salar*) occurs in both anadromous populations that frequent marine environments and spawn in freshwater, and in non-anadromous populations that are confined to freshwater habitats for their entire life cycle (Scott and Crossman, 1998; O'Connell et al., 2006). The species range spans the North Atlantic Ocean from North America to Europe. Historically, anadromous salmon were present in nearly every river that ran into the ocean, resulting in countries far from the sea, such as Switzerland, supporting local populations (Mills, 1989). Populations historically occurred as far south as Portugal in Europe and New York in the Northeastern United States. In the north of Europe, they presently extend to northwest Russia and in northern Canada to Ungava Bay (Scott and Scott, 1988; Mills, 1989; WWF, 2001). The limits of their southern distribution have moved north to the State of Connecticut in North America and Spain in Europe (WWF, 2001).

Feeding grounds for North American Atlantic salmon are believed to be located around the Grand Banks area (Reddin, 1985), in the Labrador Sea west of Greenland (Templeman, 1968) and in the Norwegian Sea between Norway and Iceland (WWF, 2001). In Europe, feeding areas include the Barents and Baltic Seas (WWF, 2001). However, the different salmon populations throughout their range are found in separate feeding grounds.

Four main genetic lineages of Atlantic salmon have been identified: West Atlantic salmon, East Atlantic salmon, Baltic Atlantic salmon and North Atlantic salmon in the Barents Sea (WWF, 2001). King et al. (2001) found that genetic differences existed within and between Atlantic salmon from North America and Europe that may correlate with life history variations.

Population

Prior to the decline of Atlantic salmon over its historic range, there numbered around 1.5 million salmon returning to eastern North America (Anderson et al., 2000). However, since the early to mid 1970's the North American and European populations have shown a decreasing trend (Parrish et al., 1998; Anderson et al., 2000; ICES, 2008a). In the southern portion of their North American range, the Atlantic salmon population in the Bay of Fundy had decreased by nearly 99% by 1999 (Anderson et al., 2000). Overall, the North American population decreased by about 75% (Anderson et al., 2000) and in the United States salmon have been eradicated in two-thirds of their habitat (King et al., 2001). Returns to southern portions of the salmon's North American range are still extremely low, and local populations are threatened with extirpation (ICES, 2008a). As a result of their decrease within the North Atlantic, salmon populations are threatened with extirpation, or are endangered or extinct in many of the original rivers throughout their range (WWF, 2001; COSEWIC, 2006; Anon, 2009). Many more are classified as critical or vulnerable (WWF, 2001).

The causes of this large decline are not certain and are likely complex due to the varying habitat and population dynamics of Atlantic salmon. Cairns (2001) presented 62 possible hypotheses concerning factors contributing to the decline of the North American population. These hypotheses considered the life stages of salmon and the various impacts encountered in each environment (freshwater, estuarine and marine). The leading 12 hypotheses include two involving fresh water life and ten involving estuarine and marine life. Of the causal factors hypothesized, five are related to life history, five to predation, one to fisheries and one to the physical and biological environment (Cairns, 2001). The possible causes of decline are variable and include pollution (chemical, organic and acid rain), urbanization, habitat degradation and over-fishing (Parrish et al., 1998; Anderson et al., 2000). Further effects related to flow reduction (Parrish et al., 1998), predation, disease, and thermal habitat changes may occur (Anderson et al., 2000) as well as impacts related to marine habitats. Despite the negative effects of each, there is no clear evidence of one primary factor driving the large decline; many of these factors may act together (Parrish et al., 1998; Cairns, 2001).

The synchronous nature of the declines among many differing river systems throughout the Atlantic salmon's range suggests common causal factors (Friedland et al., 1993; Friedland, 1998). It is likely that this decline is occurring in their shared marine environments (Anderson et al., 2000). This alarming trend in the Atlantic salmon population also suggests that continued research is needed to focus on the unknown aspects of the Atlantic salmon's life history.

Economic roles

The importance of Atlantic salmon to coastal and inland communities has been great throughout human history. In North America, salmon have been the target of large recreational and commercial fisheries since the 1600s. Prior to the collapse of the commercial Atlantic salmon fishery in Canada, there were over 10 000 commercial fishing licenses held. These were valued at over 70 million dollars (Anderson et al., 2000). Since the North American moratorium on commercial fishing, the main fisheries are now small subsistence or artisanal ones including the aboriginal and resident food fisheries as well as a strong recreational fishery (ICES, 2008a).

More recently, the global aquaculture industry for Atlantic salmon now produces over 1 million tons of Atlantic salmon per year (ICES, 2008a). This development and the declining abundance of wild Atlantic salmon effectively ended the economic viability of commercial salmon fishing, and in North America, all commercial licenses have now been retired or suspended.

The economic value now derives primarily from the freshwater recreational angling fishery (WWF, 2001). However, in some areas of the Atlantic salmon's distribution, such as Iceland, the value of the rod fishery has declined due to fewer returning 2SW fish (salmon that have spent two winters at sea). Three to four weeks of the normal fishing season have been lost (ICES, 2008a).

Management

Due to depressed populations, the current recreational fishery for salmon has been tightly regulated and low harvest levels are enforced throughout the Atlantic Ocean (ICES, 2008a). To maintain the economic benefits of recreational fishing, catch-and-release fishing has been aggressively promoted in North America, and in some jurisdictions there have been requirements for the mandatory release of large salmon which provide the bulk of the eggs in most rivers (O'Connell et al., 2006).

Proposed management practices aimed at achieving conservation goals for each river include: maintaining spawner numbers; ensuring that the genetic diversity of distinct populations stays intact (Niemelä et al., 2000); implementing catch-and-release fishing for kelts (Brobbel et al., 1996); closing angling in rivers where the conservation goals are not being met in Northern Europe; the continual phasing out of remaining net fisheries (ICES, 2008a); and the protection and listing of the vulnerable salmon populations (Anderson et al., 2000).

Success of these and other techniques are variable. The reduction in exploitation has increased adult returns and spawners in some rivers like the Miramichi River. In the 12 monitored rivers in Canada, smolt production has increased in five, decreased in two and been maintained in four, but in the United States smolt production has decreased significantly since 2006 in the one monitored river (ICES, 2008a). Seven rivers of the nine that have been monitored for more than ten years have shown a trend with no significant trends in smolt production. The other two rivers have shown a significant decreasing trend. Despite the different management measures, return rates of salmon to the rivers have not increased and conservation goals for many North American rivers are still not being met (ICES, 2008a).

Population structures

In North American rivers, the timing of the Atlantic salmon spawning run is variable. Run timing depends on both individual life-history characteristics, and environmental effects. Patterns generally vary in predictable ways among rivers. Large salmon can enter before grilse, grilse enter before large salmon, or, both enter at the same time. Some rivers may be dominated by 1SW (one sea winter) individuals, and others mostly 2SW (two sea winter) or older fish. Other rivers may have both 1 and 2SW salmon in them (O’Connell et al., 2006).

Similar to maiden fish (salmon that are maturing for the first time), the numbers of repeat spawners (salmon returning to spawn for a minimum of a second time) also predictably vary among rivers, with some having fewer and others more within the population. Sex ratios for different rivers also differ for different aged fish by geographical location, and also annually. 1SW maiden fish may be comprised of 1 to 100% females depending on the site and year, while females comprise between 50% and 90% of some stocks of 2SW fish (O’Connell et al., 2006).

The number of year classes of adult fish within the spawning run of a river also varies among rivers. For example, in the Miramichi River, where salmon runs are large and repeat spawning is relatively common, 8 – 9 age classes are found, whereas at other sites fewer age classes are present (4 to 5) (O’Connell et al., 2006).

In summary, the dynamics and life history characteristics of Atlantic salmon populations throughout the species’ range are highly variable. Population structures change continually due to natural and human effects and demonstrate everything from large continental differences to river-specific adaptations.

Life history

The life history of anadromous Atlantic salmon comprises about ten life stages, although across the species’ range variations occur in the timing and/or physical characteristic of each stage. These life stages include two in the egg stage (egg and eyed egg), three as juveniles in freshwater (alevin, fry and parr) and three that inhabit both fresh and/or marine environments (smolt, postsmolt and adult). The adult stage may then be separated into three categories (pre-spawning adult, spawning adult and kelt; Mills, 1989; WWF, 2001).

In nature, eggs incubate for about 110 days, depending on incubation temperature, and then hatch into alevins. Rearing times in fresh water to the smolt stage for juveniles without egg sacs (also known as parr) are one to five years or more before they migrate from the river to the ocean (Scott and Crossman, 1998; O’Connell et al., 2006). Parr may also develop into precocious parr. These are male parr that sexually mature and spawn during the upcoming spawning season in fall, but do not go through the physiological changes to become smolts that year. These fish may later develop into smolt in the coming years (Mills, 1989).

Smolt ages, as noted above, vary among locations, but generally increase with increasing latitude. In mid-latitudinal areas, smolts are generally two to three years of age. In more southern locations, ages as low as one year have been recorded. Further north, ages can reach up to eight years for rivers flowing into Ungava Bay (O’Connell et al., 2006). The stage during the first year of feeding in the ocean is referred to as postsmolt (Mills, 1989).

Once in the ocean, maiden spawning adult salmon generally spend one or two years at sea (1SW and 2SW fish, respectively) before returning to spawn (O'Connell et al., 2006). However, fish may stay longer, up to 3 or 4 years, prior to returning for a first spawning; some return to spawn after only a few months at sea (0SW fish; Mills, 1989; O'Connell et al., 2006). After spawning has finished, adults, now known as kelts, may die, return to the ocean before the onset of winter, or remain in fresh water until the spring thaw when they leave with the high water (Mills, 1989).

As Atlantic salmon are iteroparous (able to spawn more than once during their life span), the fish that have survived their first spawning season may subsequently return to spawn in following years (Klemetsen et al., 2003). These returning salmon are known as repeat spawners. In contrast, most Pacific salmon (*Oncorhynchus spp.*) are also anadromous, but are semelparous, spawning a single time after one to seven years of life and dying shortly afterwards. Exceptions are some male amago (*O. rhodurus*) and masu (*O. masou*) salmon in Asia, and the rainbow trout (*O. gairdneri*) (Groot and Margolis, 1991; Klemetsen et al., 2003).

For management purposes, returning Atlantic salmon adults are categorized as grilse (also termed small salmon; <63 cm fork length) which are usually 1SW fish, or as large salmon (≥63 cm fork length) that have usually spent more than one year at sea (O'Connell et al., 2006). Adults generally return to North American rivers between May and November, but can enter freshwater as early as March or April, depending on river characteristics and population dynamics (O'Connell et al., 2006). In Europe, most river entry timing is similar to North American timing; however, populations exist where freshwater entry occurs year round (ICES, 2008a).

As noted above, the returning adults may be either maiden fish or repeat spawners. Repeat spawning salmon that return to spawn in consecutive years are termed "consecutive spawners", whereas fish that skip one or more years between subsequent spawnings are termed "alternate spawners". Whether or not a repeat spawning fish returns as a consecutive or as an alternate spawner is thought to be related to the distances traveled during their feeding migration between spawning events.

Consecutive spawners return to the rivers after a period of two to five months at sea, although shorter returns of 34 and 45 days have been documented in some Newfoundland rivers (Reddin et al., 2004; ICES, 2008a). This short duration within the marine environment leads researchers to believe that consecutives travel only short distances from their home rivers (about 100 km) to recondition. They are believed to travel shorter distances than postsmolts and alternate spawners from the same river (Reddin et al., 2004; Niemelä et al., 2006). This implies that kelts becoming consecutive spawners must remain within coastal areas, and if originating from the Gulf of St. Lawrence region may remain within the Gulf.

North American alternate spawners are hypothesized to return to waters around Greenland (ICES, 2008a). They are believed to travel farther than consecutives as they spend more than one year at sea before returning to spawn (Reddin et al., 2004). Their destinations may be the known feeding grounds in the Labrador Sea and Grand Banks where kelts have been captured in previous studies (Lagueux, 1953; Reddin, 1985; ICES, 2008a). The return of these fish is dependent upon their reconditioning to energetic levels that support another spawning migration.

The time it takes to recondition varies from months to years (Lagueux, 1953) and is dependent upon many environmental and biological variables. The survival of post-spawning fish from the Miramichi River has been associated with increased abundance of prey items in the region (ICES, 2008b). This increase has resulted in an increased number of consecutive spawners returning to the Miramichi River (1 – 6 % and 1 – 17 % for 1SW and 2SW fish respectively). However, the increase in prey items has not been linked to an increase in the number of alternate spawners that do not remain in the Gulf of St. Lawrence to feed (Chaput et al., 2010). How the abundance of prey items may affect the return of alternate spawners to various rivers is not yet known.

Migration

The salmon’s migratory life begins at the smolt stage when parr go through physical and physiological changes adapted for marine survival (McCormick et al., 1999; Whalen et al., 1999). Within rivers, smolts generally move downstream in a diel fashion, resting during the day and moving at night (McCleave, 1978). Once in the estuarine environment, smolts cease exhibiting diel movements and may follow the currents and tides near the surface to coastal areas. These movements within the estuary can be passive, as the salmon follow the prevailing downstream currents in a continuous downriver trajectory to the mouth of the estuary (McCleave, 1978; Fried et al., 1978). This migration out of the estuary is relatively quick for most salmon (Thorpe, 1994). Smolt survival through the estuary is variable, and for some rivers at least, may be indicative of predator swamping (ICES, 2008a).

Research methods for studying the migratory movements of Atlantic salmon outside of their respective river systems have steadily progressed. Scientific cruises have studied the dispersal, health and biology of varying salmon age classes within the Atlantic Ocean (Templeman, 1967; Reddin and Short, 1991; Lacroix and Knox, 2005; ICES, 2008a). Studies using external markers (tags or fin clipping) on juveniles and adults benefited from the salmon fishery when it took place, as well as from captures reported at angling and salmon monitoring facilities (Belding and Préfontaine, 1961; Saunders, 1967). Belding and Préfontaine (1961) documented migratory movements of adult salmon released from Quebec’s north shore and the northern peninsula of Newfoundland. Similarly, Caron (1983) inferred the migratory movements of postsmolts exiting the Gulf of St. Lawrence from salmon caught as bycatch in herring fisheries. These studies have provided preliminary indications on a broad scale of the dispersal, migration and return of marked salmon.

Dutil and Coutu (1988) documented the capture patterns of postsmolts originating from rivers along the north shore of the St. Lawrence River system. From these capture patterns they inferred that peak movements over a single day occurred during sunrise and sunset. They also inferred that larger migratory movements away from coastal habitats occurred when sea surface temperatures (SST) decreased at the end of fall. As these postsmolts remained within the Gulf of St. Lawrence for a prolonged period (until the end of September), Dutil and Coutu (1988) suggested that salmon from North Shore Gulf of St. Lawrence rivers may linger in these waters later in the season than other populations and may even overwinter within the Gulf of St. Lawrence. Friedland et al. (1999) found that the Gulf may be used as a seasonal nursery for postsmolts, but that it reaches water temperatures nearing the lethal limit for salmon (- 0.7 ºC; Saunders et al., 1975) during the winter months.

These findings suggest that the Gulf is generally not a suitable overwintering habitat and that salmon must leave the area in order to survive the winter, unless presently unknown refuge areas are available. Current research on smolt and postsmolt migration indicates that there is an aggregation in the Gulf of St. Lawrence of postsmolts from different rivers (Miramichi, Restigouche and Grand Cascapedia) during the first few months. Travel times for fish from these rivers out of the Gulf of St. Lawrence are quick, with speeds estimated at 18-25 km/d to reach the Strait of Belle Isle (ICES, 2008a). This supports previous research by Caron (1983) that found postsmolts using the Strait of Belle Isle and Cabot Strait to exit the Gulf. Caron (1983) also suggested that juvenile salmon from the same river use both exits, but what determines this separation and the proportion of use is not known. A possible cause may be that postsmolts are following the prevailing counter clockwise currents of the surface waters caused by the outflow of freshwater from the St. Lawrence River and inflow of salt water through Cabot Strait and Strait of Belle Isle. The main currents flow out along the southern coast and in along the northern coast of the Gulf. Postsmolts may also have schooled with other postsmolts from different river systems that normally go through a specific exit.

For salmon originating outside the Gulf of St. Lawrence in southern Nova Scotia, the Bay of Fundy and the Gulf of Maine, Montevecchi et al. (1988) inferred their migratory routes from tag relocations on a Northern Gannet (*Morus bassanus*) colony to be along the southern coast and around Newfoundland to the Grand Banks area. Fish from the southern areas and the Gulf arrive in the Labrador Sea about three to four months after leaving their home rivers, creating a mixed salmon stock (Reddin and Short, 1991). Within the Atlantic Ocean, mortality is difficult to assess but is believed to occur at its greatest proportion during the first weeks at sea (Friedland, 1998). Growth, maturation and survival of postsmolts to adults has also been linked with SST (Friedland, 1998; Crozier and Kennedy, 1999).

Lear (1972) documented heavy feeding activities within the Davis Strait and Labrador Sea, indicating their importance as major feeding grounds for Atlantic salmon.

However, salmon from both North America and Europe that share feeding areas off Greenland are also suggested, at least historically, to travel between the Labrador Sea and the Grand Banks from spring until fall to feed (Martin and Mitchell, 1985; Reddin, 1985). Captured fish were mostly near the surface, suggesting this is where Atlantic salmon may spend most of their time (Templeman, 1968). However, deep dives have been documented by Halttunen et al. (2009) and Hedger et al. (2009). Within European waters, SST is believed to influence salmon migration and may even dictate the extent of their range each year within the Northeast Atlantic (Martin and Mitchell, 1985; Friedland et al., 2000). The movements documented within the Northwest Atlantic may possibly be attributed to SST in some part.

Occasionally, North American Atlantic salmon tagged at sea off the Faroese Islands have been documented to return to North American rivers (Hansen and Jacobsen, 2003). However, the majority of North American origin fish are believed to remain within the northwest Atlantic Ocean (Templeman, 1968; Reddin, 1985). For salmon remaining in the Northwest Atlantic, earlier research indicates that adults may use the southern Grand Banks as wintering and/or staging grounds; they then pass through Cabot Strait into the Gulf of St. Lawrence as early as the beginning of May in some cases (Templeman, 1968; Reddin, 1985). However, the Strait of Belle Isle may also serve as a migratory route into the Gulf for adults, although this has not yet been documented. Once the salmon are in the Gulf, their rates of travel to the rivers are relatively slow. Belding and Préfontaine (1961) through mark and recapture studies documented average straight-line rates of travel of 11.7 km/d for salmon marked with external tags off Sept-Iles, Quebec or St. Anthony, Newfoundland, and subsequently recaptured in various rivers in Quebec and Atlantic Canada.

Estuarine movements of returning salmon are variable and slower (Stasko, 1975), possibly due to a necessity for acclimation to fresh water. Smith and Smith (1997) noted that upstream movements within the Aberdeenshire Dee estuary in Scotland were dependant upon the tides and time of day, occurring mostly at night. Entry into the rivers is similarly affected by tides and time of day. Entry has been shown to occur mostly during ebb tides at night in the River Tana in Finland (Erkinaro et al., 1999; Karppinen et al., 2004). Diel patterns for both are dependent on river location. In river systems farther north where 24 hour daylight is present, Atlantic salmon did not exhibit diel patterns of movement (Thorstad et al., 2008). Reports for some North American and European stocks suggest that salmon entering the rivers earlier in the season are believed to go farther upriver than salmon entering later in the season (Saunders, 1967; Stewart et al., 2002), but what causes this is unknown (Thorstad et al., 2008).

Within the river system, migration may occur throughout the day and night (Smith and Smith, 1997; Lilja and Romakkaniemi, 2003; Karppinen et al., 2004) depending on environmental and river conditions (Thorstad et al., 2008). River migration has been broken up into three phases (Bardonnet and Baglinière, 2000; Thorstad et al., 2008). These are: 1) an initial upriver movement close to the salmon's final spawning grounds, 2) a long residency period that can include up and downstream movements known as searching and 3) a final upriver movement to the spawning grounds. However, the effects environmental variables (e.g.: water temperature, discharge) and human and natural barriers have upon migrating salmon may change with time and as the fish moves upriver (Lilja and Romakkaniemi, 2003; Karppinen et al., 2004; Thorstad et al., 2008). In general, an increased river discharge and decreased temperature will increase migration speed, but hinder it at high water levels and temperature extremes, respectively (Erkinaro et al., 1999; Lilja and Romakkaniemi, 2003; Karppinen et al., 2004; Mitchell and Cunjak, 2007). Once on the spawning grounds, salmon are energetically depleted and continue to lose lipid and tissue mass in accordance with the amount of spawning activity (Jonsson et al., 1991b; Doucett et al., 1999; Niemelä et al., 2000).

Once spawning is completed, depending on the river system, a proportion of the salmon return to the sea in late fall and early winter (Lagueux, 1953; Niemelä et al., 2000). The remaining salmon that do not leave either die or overwinter in the deep pools, lakes and backwaters of the river system above and below the tidal limits (Komadina-Douthwright et al., 1997; Niemelä et al., 2000). Overwintered kelts then leave the river over a two to five week period as the ice begins to break up (Lagueux, 1953; Niemelä et al., 2000). If these kelts survive, they return as consecutive or alternate spawners.

Tagging and telemetry

Within the North Atlantic Ocean the number of salmon tagged for research and monitoring purposes has increased over the years to 4.36 million per year in 2007 with an increased use of more advanced tagging methods (Data storage tags (DST), radio and sonic tags; ICES, 2008a). These advanced tagging methods have increased our ability not only to make inferences about Atlantic salmon movements, but to document the movements at finer resolutions.

Radio telemetry in North America and Europe has provided important knowledge on Atlantic salmon freshwater movements (Komadina-Douthwright et al., 1997; Erkinaro et al., 1999; Whoriskey et al., 2000; Karppinen et al., 2004). It allows for the monitoring of tagged fish from boat, land or air, providing detailed fine scale movements (Koehn, 2000). Research has focused on the timing of river entry and upriver movements of salmon and on potential control factors (Erkinaro et al., 1999; Karppinen et al., 2004), as well as on behavioral effects of catch-and-release (Whoriskey et al., 2000) and on the overwintering movements of kelts on the Miramichi River (Komadina-Douthwright et al., 1997). However, these tags are not suitable for studies within saline environments due to the high conductivity of the water that interferes with the tag signals (Koehn, 2000).

The use of DSTs has been implemented to document the temperatures experienced by tagged fish during migration; recapturing the fish is required to retrieve the data. Walker et al. (2000) tagged 55 Pacific salmon (*Oncorhynchus* spp.) in the Pacific Ocean and recaptured eight fish returning to rivers in Asia and North America. Similarly, DSTs have been used on Atlantic salmon in North America and Europe to document the temperatures experienced by migrating adults in coastal waters (Reddin et al., 2004; ICES, 2008a). These tags can also be equipped with geolocation capabilities (ICES, 2008a).

These tagging methods have given insight into the broad scale movements of salmon between habitat types (river to ocean) (Belding and Préfontaine, 1961; Caron, 1983) as well as into the finer scale movements within river systems (Whoriskey et al., 2000). Our understanding of their environment has improved with the use of DSTs (Reddin et al., 2004). However, apart from the use of satellite telemetry, which is very costly (Koehn, 2000), these methods are less suited to answering the fine scale problems that span the freshwater, estuarine and marine environments of Atlantic salmon and are poorly suited to addressing potential areas of decline.

There is a need to obtain information on the natural behaviors and migration of Atlantic salmon with improved methods of data collection at sea (Reddin et al., 2004). The development of acoustic telemetry has enabled this type of data gathering. The associated costs have decreased as the methodology has evolved, making it ideal for long-term, widespread studies of aquatic organisms through projects such as the Ocean Tracking Network (OTN) that is progressively installing acoustic receiver arrays within the northwest Atlantic Ocean (ICES, 2008a).

Early acoustic telemetry technologies for Atlantic salmon research were primitive. These have subsequently been refined and tags much reduced in size. Early tags were too large to place in most juvenile salmon (parr and smolt) (Lacroix et al., 2004). They had a short battery life (≈ 30 days) and a short detection range (50 to 150m), depending on environmental conditions, and they worked poorly in saline environments (Moore et al., 1995; Carr et al., 1997). The receivers were multi-channel, creating limitations to its uses (Heupel et al., 2006).

The present tags have a pulsing signal with “on” and “off” times programmed for varying lengths. This has extended the life span of the tags to in some cases many years (Hightower et al., 2001; Lacroix et al., 2004). Each tag emits a unique ID that can then be detected and stored by the single channel receivers currently used (Heupel et al., 2006; Whoriskey et al., 2006). The reception distance of the tag signals has increased in distance, up to 2 km in some cases. Current tags are well suited to saline environments (Whoriskey et al., 2006; ICES, 2008a).

The methods by which the tags are attached to the salmon have also improved. There are three primary methods used to attach sonic tags to salmon of various ages and sizes: external, stomach insertion through the mouth, and peritoneal; each method has its own benefits and drawbacks (Moore et al., 1990).

Stomach and peritoneal attachments have been used extensively in Atlantic salmon migratory research (Stasko, 1975; Fried et al., 1978; Carr et al., 1997; Whoriskey et al., 2006; ICES, 2008a). The insertion of tags into the stomach is rapid and simple, but there is a greater risk of losing the tags over short periods through regurgitation. External attachments increase the drag on the fish and may be lost to snags on debris within their environment. Surgical implantation of the tags into the peritoneal cavity is more complex, but is best suited for long-term telemetry studies and is considered the norm (Moore et al., 1990). Standard operating procedures for Atlantic salmon are similar to Whoriskey et al. (2006) and have been extended and modified for other species such as American eels (*Anguilla rostrata*, Carr and Whoriskey, 2008) and Atlantic cod (*Gadus morhua*, Brooking et al., 2006).

It is very important to ensure that tagged fish exhibit normal behaviors and are not negatively affected by the tagging procedures or the tags. There have been many studies looking at the potential impacts of tagging on juvenile and adult salmon (Moore et al., 1990; Thorstad et al., 2000; Lacroix et al., 2004). Both Moore et al. (1990) and Thorstad et al. (2000) found no ill effects of the tagging procedures or tags on the swimming performance and capacity, or the buoyancy, of juvenile or adult Atlantic salmon. Lacroix et al. (2004) did find a small decrease in swimming performance in smolts over a short duration. Minimal negative impacts upon feeding behavior were also documented for the first eight hours post surgery in smolt with initial weight loss that then rebounded to normal levels (Moore et al., 1990; Lacroix et al., 2004). Little internal stress response to the tags was found when dead smolts were analyzed, although a slight rubbing of the tags against the peritoneal wall caused minor irritations (Moore et al., 1990). Tags were either encapsulated against the peritoneal wall by new tissues or expelled from the fish through the abdominal wall with no negative effects on the fish during the entire study period of almost a year (Moore et al., 1990, Lacroix et al., 2004). Mortalities associated with the procedures and tags are minimal, with most deaths occurring in smolt between 19 and 40 days. These deaths were linked to the larger test tags as opposed to the smaller ones deployed in the field in same sized fish (Lacroix et al., 2004).

Acoustic telemetry has been implemented for different purposes using various techniques. It has been applied to scientific research focusing on fish migration, and to population management techniques and concerns such as assessing natural and fishing mortality in striped bass (*Morome saxatilis*) (Hightower et al., 2001; Heupel et al., 2006). The technology can be used on any aquatic organism to which a tag can be attached, and properly sized tags do not impair it physically or behaviorally. Acoustic telemetry has been used on teleosts, crustaceans, sharks and cephalopods (Heupel et al., 2006).

There are two main detection options used in sonic telemetry for passive tracking with fixed receivers, depending on project objectives; these are curtain, and grid arrays. Curtain arrays “block off” the passage to a given area, such as the exit of a bay, which a fish must pass through to reach its destination. Grid arrays are a series of receivers placed in a grid pattern in order to determine where the fish is in a given area (Heupel et al., 2006). These two systems can be further refined and or combined to meet the needs of specific projects (see details in Heupel et al., 2006).

Sonic telemetry has been used to actively and passively track Atlantic salmon (Fried et al., 1978; McCleave, 1978; Whoriskey et al., 2006; Lacroix, 2008; Hedger et al., 2009). Curtain arrays are less labor intensive (Heupel et al., 2006) and have been successfully implemented in rivers, bays and coastal waters in the Atlantic Provinces to study salmon migration (ICES, 2008a; Hedger et al., 2009). The improvements in acoustic telemetry have permitted its use in deeper saline environments (Koehn, 2000). It has become a useful tool for the coastal and continental shelf tracking of aquatic organisms as it is expanding throughout the Atlantic Ocean (Heupel et al., 2006; ICES, 2008a).

This technology has the potential to open up the “black box” that is the oceanic life of Atlantic salmon. In a workshop summarizing research strategies focusing on the cause of the Atlantic salmon population decline, O’Neil et al. (2000) listed four questions that could be answered in whole, or part, by telemetry. The proposed questions were: determining size-dependant survivorship, documenting coastal migration routes, documenting Atlantic salmon distribution in the Atlantic Ocean, and estimating survival rates of salmon during their voyage from the river to the ocean. Various researchers are currently conducting studies addressing these questions at present.

The advancement and expansion of acoustic telemetry continues to lead researchers closer to locating areas and causes of marine mortality, to locating areas of salmon congregation in the ocean during migration, feeding and overwintering (ICES, 2008a), and to documenting fine scale movements that other current cost-effective technologies cannot.

The importance of kelts

Since the early 21st century, research focusing on Atlantic salmon migration has begun to expand out of the river and estuary systems and into coastal and oceanic habitats (ICES, 2008a). This is relatively recent, however; little is still known about the Atlantic salmon's exact migratory movements and the areas that encompass them. Knowledge of the broad coastal movements and ocean migration routes, to and from their home rivers, and of the different marine phases of the Atlantic salmon's life cycle, in particular the postsmolt and kelt phases, is lacking. We also know little of the distribution of the different age classes of Atlantic salmon throughout their feeding and overwintering grounds in the Atlantic Ocean and of the factors that govern their presence in these areas. Our understanding of fine-scale movements and associated survival rates in the marine environment is also poor.

Of particular importance is the minimal knowledge we have of repeat spawning salmon and the associated kelt stage. This particular life stage is understudied and requires further research to determine the significance kelts have in the Atlantic salmon population. Much of the research on kelts has occurred in Europe (Jonsson et al., 1991a; Bardonnet and Bangliniere, 2000; Niemelä et al., 2000; Niemelä et al., 2006; Halttunen et al., 2009), with additional work occurring in North America (Lagueux, 1953; Komadina-Douthwright et al., 1997; Reddin et al., 2004; Hubley et al., 2008; ICES, 2008a; Hedger et al., 2009).

The kelt portion of the Atlantic salmon's life cycle is the critical stage of the life cycle for salmon that become repeat spawners because the survival of these kelts is directly related to the number of returning repeat spawners. However, current knowledge of the stage is of a basic nature regarding biology and migration. There is a lack of information surrounding aspects of migratory pathways such as routes, destinations, and mortality rates (where and when rates are highest and what affects them; Friedland et al., 1998, 2000). Further research is also needed concerning migration timing and duration of repeat spawners and the parameters that play a role in the reconditioning of kelts (Friedland et al., 1998; Niemelä et al., 2000).

The decline in the North American Atlantic salmon population has led to increases in research targeting aspects that may help determine and, in turn, reduce the progressive declines in the population. Niemelä et al. (2000) state that kelts are an important safeguard to failed spawnings in a given year and to mass ocean die-offs that may occur. Kelts are also important to population abundance and as contributors to genetic diversity in each river system (Niemelä et al., 2000), as repeat spawners have greater fecundity, providing more eggs than maiden fish to a given spawning class (O'Connell et al., 2006). Kelts may spawn in consecutive or in alternate years, but it is not known what regulates these different spawning adaptations. The Miramichi River system, among others, supports a large kelt sport fishery in spring and research is needed to ensure that these fish are not negatively affected by the fishery (Brobbel et al., 1996) and that they remain an integral part of the communities that depend on them. Gaining knowledge of the migratory routes and survival rates of kelts is also important in ensuring the Atlantic salmon's continued presence.

The kelt stage of Atlantic salmon is the focus of this thesis. Acoustic telemetry was used to address some of the knowledge gaps mentioned above. There were five main objectives: 1) to provide detailed descriptions of kelt survival and movements through the Miramichi River estuary, 2) to document the survival-to-return of repeat-spawning kelts, identifying both alternate and consecutive spawners, 3) to document environmental factors within the estuary faced by migrating kelts, 4) to document possible effects of catch-and-release fishing on kelts, and 5) to document the ocean migration routes of kelts originating in the Miramichi River.

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CONECTING STATEMENT

Chapter 1 reviewed the pertinent literature needed to understand the past and present status of Atlantic salmon and the species management. It has also focused on research identifying knowledge gaps and areas of needed research especially the kelt life stage. The second chapter examines the migration and survival of kelts as they exit the Miramichi estuary and discusses the importance of this migratory stage to their overall survival.

CHAPTER 2: THE ESTUARINE MOVEMENTS AND SURVIVAL-TO-RETURN OF ATLANTIC SALMON KELTS FROM THE MIRAMICHI RIVER SYSTEM

ABSTRACT

Sonically tagged Atlantic salmon kelts exited the Miramichi estuary quickly with a high survival rate. In 2008 and 2009 combined, 94 % (n = 100) of kelts were detected exiting the estuary. Eleven of these fish subsequently returned as repeat spawners (seven consecutives, four alternates) and none used the estuary for overwintering after spawning. The majority of kelts leaving the system spent more time in the upper reaches of the estuary compared to the middle and bay areas. Average speeds of travel varied between years, but increased as kelts neared the exit to the Gulf of St. Lawrence. During migration, depths and temperatures of travel varied with ranges of 0 to 19.4 m and 4.7 to 15.1 °C respectively. Estuarine survival of kelts is high, suggesting that the effects of catch-and-release angling are negligible. Due to the low returns of repeat spawners, further research is needed to determine where the losses of adult salmon are occurring and any contributing factors.

INTRODUCTION

Atlantic salmon (*Salmo salar*) populations have declined precipitously in North America over the past three decades (ICES 2009), and the conservation and resilience of these populations are increasingly dependent upon iteroparous individuals that spawn more than once in their lifetime (Chaput et al. 2010). In certain river systems adults may return to spawn up to seven times during their life span (Chaput and Jones 2006; O'Connell et al. 2006).

Those that have survived spawning are termed kelts. Kelts are energetically-depleted, and return to the sea in late fall or early spring to put on additional growth and recondition in preparation to become repeat spawners in the future (Jonsson et al. 1991b; Niemelä et al. 2000; O'Connell et al. 2006). These repeat spawners may be either consecutive (spawn every year) or alternate (skip one or more years between successive spawnings) spawners. A given individual may alternate between the consecutive and alternate patterns of reproduction over its lifetime (Jonsson et al. 1991a; Niemelä et al. 2000; O'Connell et al. 2006). Depending on the river system, repeat spawners make up a varying proportion of the returning salmon (O'Connell et al. 2006). Repeat spawners are important to these populations because larger females supply more eggs than the younger, smaller individuals of the spawning class of a given year because the number of eggs produced is related to body size (Chaput et al. 2010; Niemelä et al. 2006). They also act as genetic contributors to multiple spawning classes (Ducharme 1969) and provide potential safeguards against population crashes at sea and repeated reproductive failures (Ducharme 1969; Niemelä et al. 2000).

Due to their weakened condition, we expect that kelts are most vulnerable to mortality in the period following spawning, and during the early portion of their return migration to the ocean. Despite the potential importance of this period, there has been very limited research on kelts overwintering in and exiting river systems in North America and Europe (Komadina-Douthwright et al. 1997; Niemelä et al. 2000). The studies of Hubley et al. (2008), Halttunen et al. (2009) and Hedger et al. (2009) used acoustic telemetry to track kelt movements, depths of travel and survival during spring migration. However, the short duration of these studies and the limited battery life of the tags used did not permit an extensive study of the adult's full life cycle (kelt to spawning adult). The feasibility of acoustic telemetry to study smolt survival and migration from fresh water to the Atlantic Ocean has also been documented (Moore et al. 1995; Lacroix and McCurdy 1996; ICES 2008a).

The Miramichi River system supports the largest Atlantic salmon population in eastern Canada (Chaput et al. 2001) with population estimates at 49, 000 (29, 840 grilse and 19, 910 salmon) salmon returning to the river system in 2007 (Chaput et al. 2010). The Miramichi population of spawning adults is comprised of eight to nine distinct age classes (Chaput and Jones 2006). This is due to differing juvenile maturation rates and a recent increase in the numbers of repeat spawning fish (Chaput and Jones 2006; O'Connell et al. 2006). At present, the majority of these fish are consecutive (spawning in consecutive years) rather than alternate (skipping one or more years between subsequent spawning) spawners (Chaput and Jones 2006) and most repeat spawners of all types first matured as 2SW rather than 1SW salmon (Chaput and Jones 2006).

This study used acoustic telemetry to document survival and residence times of Miramichi River fish passing through the river's estuary. All fish tagged were captured by anglers during the annual spring kelt fishing season on the river. The main objectives of this study were: 1) to provide detailed descriptions of kelt survival and movements within the estuary, 2) to document survival-to-return of repeat spawners, 3) to document environmental conditions within the estuary faced by migrating kelts and 4) to infer possible long-term effects of catch-and-release fishing on kelts.

METHODS

Study site

The Miramichi River system drains a total area of 14,000 km^2 and is composed of two principle branches: the Northwest (NW) branch (draining an area of 3,900 km^2) and the Southwest (SW) branch (draining an area of 7,700 km^2; Chaput et al. 2000). The confluence of these two branches occurs in the estuary just upstream of Beaubears Island (Figure 1). From here the estuary runs in a single main stem for 52 km past Sheldrake Island to the exit from the estuary (Barrier Islands) to the Gulf of St. Lawrence. The Miramichi estuary covers an area of 300 km^2, with tidal effects evident up to 80 km upstream into the Northwest and Southwest branches at their respective heads of tide. The estuary ranges from less than 0.5 km wide in some areas to 22 km wide at its exit to the Gulf of St. Lawrence. The average depth is 5 m with a principle channel 7.6 m deep dredged from Newcastle to the Barrier Islands (Robichaud-LeBlanc et al. 1998).

Hydrophone deployment

Hydrophones (Model VR2: single channel monitoring receivers manufactured by Amirix/Vemco, Halifax, NS) were moored at different positions within the estuarine portion of the Miramichi River from the head of tide to the Outer Miramichi Bay area. The receivers at a given position were placed to provide complete detection coverage of the channels that fish could pass through. Thus quantitative estimates of the numbers of fish surviving to each point could be calculated. Receivers were positioned as soon after ice breakup as feasible from April 24 to May 10, 2008 (n = 41). The VR2's were placed starting at the head of tide area of each branch (Northwest (NW), Sutherland Brook; Southwest (SW), Quarryville) and stretching to Middle Island. Additional units were placed between Middle Island and Sheldrake Island, among the Barrier Islands and along the inner and outer Miramichi bay areas (Figure 1). The units in the inner and outer bay areas were removed between August 14 and 19, 2008. The receivers remaining in the estuary between the two heads of tide and Sheldrake Island were removed on October 6 and 7, 2008.

A total of 12 units were placed in the estuary on October 6 and 7, 2008, before the summer units were removed, to overwinter until spring 2009. These were suspended on a buoy in the water column about 1 m above the anchor on the river bottom. This minimized the probability of the unit being covered by bedload sediments, being snagged by floating debris, or having its float encased in winter surface ice. Receivers were placed near the locations of the summer units from Red Bank and Millerton in the Northwest and Southwest branches respectively to Bartibog River within the main branch. Overwintering units were retrieved between April 24 and August 30, 2009.

Twelve units were re-deployed on August 4 and 5, 2009 for the fall monitoring period at the same locations as the 2008/2009 overwintering units in 2008. Thus, receiver coverage in the estuary was continuous for the duration of the study.

Spring and summer receivers were then deployed from April 24 to May 13, 2009 (n = 39) in the same locations as those in 2008. Units were placed prior to the removal of the 2009/2009 overwintering units.

Kelt capture

All fish used in this study were captured by anglers fly fishing for kelts (single barbless hook) in a designated spring season for this activity. Anglers were not supervised by our biological team during their fishing, and notified the biological team of captures of fish that they were willing to provide by sight, radio or cell phone. We then picked the fish up in a boat equipped with holding tank filled with fresh river water, and moved them back to our surgical site. Here, kelts were moved to a large aerated Xactic tank filled with fresh river water to recuperate from the stresses induced by angling and transport for at least 15 minutes.

Kelt tagging

Surgical implantation of acoustic tags into the kelts (approved by the McGill University animal care committee) took place near the head of tide on both the Northwest (Red Bank bridge) and Southwest (Quarryville bridge) branches of the Miramichi Estuary. Fifty kelts were tagged in each of 2008 and 2009.

Different tag models were used, depending on our resources, fish size, and our objectives. All tags used were coded with a unique individual ID. In 2008, 20 V13’s (13 mm in diameter, 36 mm long, 6 g in water) and 10 V16’s (16 mm in diameter, 96 mm long, 16 g in water) that emitted an ID only, were deployed. In addition, in 2008 20 V16 tags with an ID and temperature and pressure sensor (T/P) were also used. These tags were distributed among fish captured in the two branches of the river, with 20 V13’s, nine coded V16’s and 12 coded T/P V16’s placed on fish in the Northwest branch. The Southwest branch had no fish tagged with V13’s, one fish with a V16 tag and eight individuals marked with T/P V16 tags. In 2009, 50 V16 tags (45 ID only, and five with ID and T/P readers) were used. A total of 22 tags with ID only and three coded T/P tags were implanted into fish from the Northwest branch. On the Southwest branch, 23 kelts were tagged with ID only tags and two with T/P tags (see Appendix 1a, b).

Tagging on the Northwest branch took place on May 7 (n = 11), May 9 (n = 14) and May 14 (n = 16), 2008. Tagging on the Southwest branch took place on May 8 (n = 2) and May 13 (n = 7), 2008. In 2009, tagging on the Northwest branch took place on May 8 (n = 25) and tagging on the Southwest branch took place on May 6 (n = 11) and May 7 (n = 14).

After recuperating from the initial stresses of angling, kelts were then anaesthetized in a mixture of water and clove oil (concentration of 40 mg/L). Once sufficiently anaesthetized (loss of equilibrium; absence of reactions to external stimuli) they were weighed (kg), measured (fork length, cm), scale sampled (for age determination), sexed (noted as male, female or fish whose sex could not be identified (“unknown”)) using secondary sexual characteristics and placed ventral side up into a U-shaped surgery board lined with wet mattress foam. All equipment used for surgery was first disinfected with diluted Wescodyne. During surgery, all surgery gear was disinfected in a mixture of distilled water and Furacin prior to each fish operation while tags were disinfected in 90% alcohol, rinsed and dried. A 2.5 – 3 cm incision was then made with a curved scalpel blade along the abdomen, slightly adjacent to the midline and just anterior of the pelvic girdle. The tag was then inserted lengthwise into the interperitoneal cavity. The incision was sutured closed with two to three interrupted sutures using a number two suture thread and curved needle. During the entire surgical procedure, the gills of the fish were continuously irrigated with fresh river water. In the rare instances where the fish showed any sign of reviving during surgery, we replaced the water being used to irrigate the gills with a clove oil solution in order to deepen the anaesthesia. After surgery was completed (total time from removal from the anaesthetic bath to return to the recovery crates was 2 to 5 min) kelts were placed in large wooden flow-through recovery crates in the river. Kelt recuperation time from the effects of the anaesthetic was approximately five minutes. After a minimum of two hours of recovery, the kelt was released back into the river at the surgery site. This let us confirm that no immediate mortality occurred from the surgery or from delayed reaction to the stress of angling.

Environmental monitoring

Following the release of the kelts, on various dates environmental conditions (water temperature (ºC), salinity (ppt) and dissolved oxygen concentrations (% saturation) were measured with vertical profiles at fixed stations using a Hydrolab (DS5, Campbell Scientific; Figure 1). At these locations, surface to the bottom profiles were taken in order to locate vertical stratification in temperature and dissolved oxygen, and to document the location of the salt wedge in the estuary. In 2008, sampling began on May 15 from the head of tide receivers on the Southwest and Northwest branches to those located at lower Beaubears Island (Figure 1). Sampling ended on May 21 at VR2's located from Nordin to Sheldrake Island and the three exits of the estuary (Neguac Channel, Portage Channel and Huckleberry Gully). In 2009, sampling took place on May 13 at units located from Nordin to Sheldrake Island and the three exits of the estuary (Neguac Channel, Portage Channel and Huckleberry Gully). It ended on May 14 at locations from the head of tide receivers on the Southwest and Northwest branches to those located at lower Beaubears Island (Figure 1).

Data retrieval

Receivers were downloaded periodically throughout the summers of 2008 and 2009. The information stored in a download consisted of the fish ID, time and date of detection as well as the temperature and depth the fish was at.

All summer units were removed by October in 2008 and 2009. Three units were lost before final retrievals in 2008 (Douglasstown 1, Doyals Brook and Escuminac 2), and one unit in 2009 (Millerton 1). Little to no data was lost due to the missing receivers as previous downloads were taken from some units or a second unit was in range of the missing one, so coverage of the designated area remained complete.

Overwintered receivers (from 2008/2009) were retrieved during the spring and summer of 2009 when conditions were suitable. The submerged units were grappled to the surface or on occasion retrieved by a diver. All 12 units in each year were successfully retrieved; however, one unit (Sutherland Brook, 2008) had malfunctioned and provided no data. Recovery of the 2008 overwintered units was done after the spring/summer units for 2009 had been deployed, to ensure that there was continuing receiver coverage to monitor tagged fish.

Analyses

Statistical analyses were conducted using parametric and non-parametric tests as appropriate, following Zar (1999). For parametric and non-parametric tests, groupings of grilse and salmon were of combined sexes (male, female and unknown sex) while groupings of males and females excluded those of unknown sex and were composed of a combination of ages (grilse and salmon).

The estuary was divided into four sections, separated according to their geographical distinctions (Northwest branch, Southwest branch, Main branch and Inner Bay). Three sections were used for the analyses; 1) the Northwest or Southwest branch (head of tide region to Beaubears Island), 2) the Main branch (Beaubears Island to Sheldrake Island) and 3) the Inner Bay (Sheldrake Island to the Barrier Islands; Figure 1). The expected amount of time kelts spent within each section was weighted by channel length of the section in question. A chi square goodness-of-fit test was used to compare the amount of time kelts spent in different sections of the estuary when exiting and entering the system.

Travel times (the amount of time a kelt spent within a particular area) was calculated by taking the time of release or their first detection on a given receiver to the last detection of a given receiver. Kelts that frequented a given area more than once had each individual measure of time added together to give a total amount of time within the designated area. All distances were measured as straight line distances. Speeds of travel were obtained using the calculated travel times over the measured straight line distances.

When calculating survival within the estuary, a kelt was considered dead when continuous detections were recorded at the same location for an extended period of time (> 2 weeks, stationary tag) or when the kelt was not located up or downstream of its last location (excluding units at the estuary exit). Kelt depths were categorized per kelt into one meter increments from the surface (0 m) to their deepest depth. The number of depth detections was recorded for each depth increment. A “dive” was considered to occur when the depth obtained from a kelt was deeper than the majority of depth detections.

RESULTS

In 2008, tagged kelts (all ages and sexes combined) averaged 67.1 cm fork length (n = 50; range 53.4 – 89.3 cm) and had mean weights of 2.1 kg (n = 39; range 0.8 – 4.35 kg). Condition factors (K) ranged from 0.45 to 0.77, and averaged 0.61. A total of 30 1SW grilse and 20 2SW salmon were tagged (21 males, 25 females, four unknown). In 2009, kelts had an average length of 62.6 cm (n = 50; range 55.4 – 92.5 cm) and weight of 1.6 kg (n = 49; range 0.9 – 5.7 kg). Average K was 0.63 (range 0.53 – 0.75). A total of 44 1SW grilse, four 2SW and two 3SW salmon were tagged (33 males, 15 females, two unknown; see Appendix 1a, b for details). All kelts were maiden spawners when tagged except for the two consecutive 3SW spawners tagged in 2009.

Survival

In 2008, kelt survival from the release point to the exit of the estuary was 95 % (39/41) and 100 % (9/9) for the Northwest and Southwest branches, respectively; the combined survival was 96 % (48/50). Survival in 2009 was similar; 92 % (23/25) each for kelts from the Northwest and Southwest and combined (46/50) branches. There was an overall survival of 94 % for the two years combined. Of the six dead kelts detected over the two years, half were male grilse (one in 2008, two in 2009) and half were female salmon (one 2SW in 2008, one 2SW and 3SW in 2009).

Kelt mortalities occurred at varying positions in the estuary. Three kelts died within the Northwest branch (Millstream area – 2, Eel Ground area – 1; all three had stationary tags), one in the Southwest branch (before Quarryville, kelt never detected on any receivers) and two within the main branch (the area between Middle Island and Bartibog River; both had stationary tags; Figure 1).

In the two years of the study, 11 kelts returned to spawn once. Of these, one female salmon was captured during the aboriginal food fishery near the Eel Ground area in the estuary. All three repeat spawners that returned in 2008 survived the spawning period and overwintering to exit the estuary in 2009. Two of these returned for a second time in 2009 as consecutive spawners. It is not known if the remaining seven fish that returned to spawn survived the winter to exit the estuary.

Correlations between the distance kelts traveled from release to estuary exit and their survival within the estuary system (Spearman's rho, $p < 0.01$) showed that mortality significantly increased with distance travelled. This correlation was seen in kelts released from the Northwest branch in 2008 ($r = - 0.932$, $p < 0.01$) and 2009 ($r = - 0.775$, $p < 0.01$) as well as from the Southwest branch in 2009 ($r = - 0.802$, $p < 0.01$). There were no mortalities for kelts released from the Southwest branch in 2008.

ANOVA were used to test for the effects of different biological parameters (sex, age, length, weight and K, or sex, age, length excluding weight and K) upon kelt survival. Kelts of unknown sex were excluded from these analyses.

In 2008, none of the biological variables significantly affected survival for kelts released from the Northwest branch when tested together ($p > 0.05$; $n = 27$). Significant results were found for age ($p < 0.05$) and length ($p < 0.05$) when tested with sex ($n = 37$). Between age and length, age had a slightly greater effect on survival than length when comparing the percent their respective sums of square makes up of the corrected total (13.9 % and 12.3 % respectively) for ANOVA. No mortalities were recorded on the Southwest branch in 2008, so no analyses were carried out.

In 2009, none of the biological variables significantly affected survival for kelts released from the Northwest branch when tested together ($p > 0.05$; $n = 23$). Tests on sex, age and length in a separate group were not conducted as all kelts had a recorded weight and K. Even though mortalities were recorded for kelts in 2009 from the Southwest branch, there was insufficient variation in the data for analysis.

Time spent in the estuary

Goodness-of-fit tests calculated for each individual kelt in 2008 ($n = 48$) and 2009 ($n = 42$) showed that they did not spend an equal proportion of time (weighted for distance) within the three separate sections of the estuary downstream from their respective release locations ($X^2_{\text{calculated}}$ value > df = 2, $p = 0.05$; see Appendix 2a, b for details; Northwest or Southwest branch, Main branch and Inner Bay) during their seaward migration.

All kelts released from the Southwest branch spent significantly more of their time within the Southwest branch (24.5 km) in 2008 (average 8.9 d, range 3.1 – 16.6 d; average 2.8 km/d, range 1.5 – 7.9 km/d) compared to the main branch (24.2 km; average 1.5 d, range 0.3 – 2.8 d; average 16.1 km/d, range 8.6 – 80.6 km/d) and inner bay (24.7 km; average 1 d, range 0.5 – 1.7 d; average 24.7 km/d, range 14.5 – 49.4 km/d). Similar results were obtained in 2009, with time spent in the Southwest branch being significantly longer (average 6.3 d, range 2.9 – 11.1 d; average 3.9 km/d, range 2.2 – 8.4 km/d) compared to time spent in the main branch (average 0.9 d, range 0.4 – 1.6 d; average 26.9 km/d, range 15.1 – 60.5 km/d) and inner bay (average 0.9 d, range 0.4 – 3.2 d; average 27.4 km/d, range 7.7 – 61.8 km/d). For kelts released from the Northwest branch (22 km) in 2008, 84.6 % (33/39) spent the majority of their time in that section (average 8.8 d, range 3.1 – 18.5 d; average 2.5 km/d, range 1.2 – 7.1 km/d). Similarly, in 2009, 95.2 % (20/21) of the fish spent most of their time in the Northwest Branch (average 6.2 d, range 2.3 – 12.8 d; average 3.5 km/d, range 1.7 – 9.6 km/d). The remainder of the kelts in 2008 spent 5.1 % of their time in the main branch and 10.3 % of their time in the inner bay respectively. In 2009, the lone kelt spent most of its time in the inner bay.

There are indications that kelts hold in a small area near the head of tide in each branch. Within the Northwest and Southwest branches in 2008, 76.9 % (30/39) and 88.9 % (8/9) of kelts respectively spent more time in the short stretch of the estuary between their respective release site and the first receivers downstream in each branch. The remainder of the kelts spent more time downstream of the first receivers in each branch. Similarly, kelts in 2009 from both branches (85 % (17/20) – Northwest, 95.5 % (21/22) – Southwest) spent more time between the release site and the first receiver rather than the downstream portions of each branch.

Because most kelts spent a large proportion of time within a small area of the Northwest and Southwest branches prior to their detection at the first receivers downstream of each release site, the Chi-square goodness-of-fit test was re-run excluding the time kelts spent between their release site and the first receiver. This was done to remove any possible biases of recovery upon their migration as kelts began to move actively downstream once detected upon the first receivers. Kelts again did not spend an equal proportion of time within the three sections of the estuary (see Appendix 2a, b for details). During both years more kelts from both branches still spent, on average, more time within the upper sections of the estuary (Northwest and Southwest branches). The number of kelts spending more time in the Northwest and Southwest branches decreased when the time prior to first detection was removed. In 2008, a greater percent of kelts from the Southwest branch spent longer periods of time within that section 55.5% (5/9) compared to the main branch 33.3 % (3/9) and inner bay 11.1 % (1/9). From the Northwest branch, 53.8 % (21/39) remained in that section for a longer period compared to the main branch 20.5 % (8/39) and inner bay 26.6 % (10/39). In 2009, more kelts remained in the Southwest branch for a longer time 9/22 (40.9 %) than in the main branch 6/22 (27.3 %) and inner bay 7/22 (31.8 %). The same was seen for kelts from the Northwest branch (Northwest branch, 9/20 (45 %); main branch, 5/20 (25 %); inner bay, 6/20 (30 %)).

A low percentage of kelts occasionally swam into the opposite branch from which they were released (8.3 % (4/48) in 2008 and 26.1 % (12/46) in 2009). The amount of time these kelts spent within the opposite branches was significantly lower than within their originating branch in both years ($p < 0.05$).

Travel time and speed

The time it took kelts from both branches in 2008 and 2009 to exit the estuary after their release was significantly different ($p < 0.05$). In 2008 and 2009, kelts took on average 13 days (5.1 – 28.7 d) and 8.5 days (3.6 – 17.8 d) respectively post-release to exit. Average time kelts from both branches took to exit the estuary from the first receiver reading (1.1 km and 3.24 km downstream of the release sites in the Northwest and Southwest branches respectively) decreased to 6.8 days (2.3 – 19 d) in 2008 and 3.4 days (1.7 – 12.5 d) in 2009 indicating that large amounts of time are spent near the head-of-tide area before kelts reached the first receivers.

From release, the time kelts from the Northwest branch spent in the estuary before exit was similar to those from the Southwest branch ($p > 0.05$) in 2008 (Northwest average 13.4 d (5.3 – 28.7 d); Southwest average 11.4 d (5.1 – 18.6 d)) and 2009 (Northwest average 8.7 d (3.6 – 17.8 d); Southwest average 8.3 d (4.8 – 12.7 d)). From both branches combined, female kelts on average were in the estuary for similar amounts of time than males in 2008 (13.6 d and 11.8 d respectively; $p > 0.05$) and 2009 (8.8 d and 8.3 d respectively; $p > 0.05$). This was similar for salmon and grilse in 2008 (13.9 d and 12.4 d respectively; $p > 0.05$). In 2009, salmon spent more time in the estuary than grilse (11.9 d and 8.2 d, respectively; $p < 0.05$).

Travel time between the first detection on the first receiver in each branch and the estuary exit were compared. In 2008, no significant differences ($p > 0.05$) were seen between kelts from both branches (Northwest – 7.3 d, Southwest – 4.4 d) or grilse and salmon (all sexes; 6.3 d and 7.5 d respectively). However, females took significantly longer to exit the estuary than males (all ages; average 7.6 d versus 5.3 d respectively, $p < 0.05$). In 2009, no significant differences ($p > 0.05$) were seen between kelts from the Northwest and Southwest branches when the two were compared (4.5 d and 3.4 d respectively), males and females (all ages; 4.2 d and 3.3 d respectively), or grilse and salmon (all sexes; 3.7 d and 6 d respectively).

The average speed of travel from release, for kelts from both branches, to the estuary exit was 6.5 km/d (2.4 – 14 km/d) in 2008 and 9.3 km/d (3.9 – 18.9 km/d) in 2009. Their calculated travel speed more than doubled, when their speed of travel was measured from the first detection on the first receiver in each branch to the first detection on the estuary exit, to speeds of 14.5 km/d (3.6 – 28.9 km/d) in 2008 and 21 km/d (5.2 – 40.6 km/d) in 2009. In both instances, kelts in 2009 traveled significantly faster ($p < 0.05$) than those in 2008.

In 2008, average speeds of travel from release to estuary exit for males and grilse (7.3 and 7.1 km/d respectively) were similar to females and salmon (6.1 and 6 km/d respectively; $p > 0.05$). The same was seen in 2009 for males and females (9.5 km/d and 8.9 km/d respectively; $p > 0.05$). However, grilse traveled faster than salmon (9.6 km/d versus 6.3 km/d; $p < 0.05$). There were no significant differences ($p > 0.05$) in speed of travel from the first receiver between kelts from the Northwest and Southwest branches in 2008 (average 13.8 and 17.5 km/d respectively) and 2009 (average 20.2 and 21.7 km/d respectively). The same was observed for grilse and salmon in 2008 (average 14.5 and 14.5 km/d; $p > 0.05$) and 2009 (average 21.2 and 18.6 km/d; $p > 0.05$) and males and females in 2009 (all ages; average 21.2 and 20.1 km/d; $p > 0.05$).

In 2008, males traveled significantly faster than females (average 17.5 versus 12.4 km/d; $p < 0.05$).

All three kelts that returned to spawn in 2008 exited the estuary in 2009 after detection on the first receiver in each branch within 2.8 and 8.3 d (average 6.2 d) at speeds between 8.3 and 23.7 km/d (average 13.5 km/d). The speed of travel for these three kelts was not significantly different from kelts tagged in spring 2009 ($p > 0.05$).

Repeat spawners

Three of the 48 (6.3 %) kelts that left the river system in spring 2008 returned as repeat consecutive spawners in the fall of 2008. All were female salmon, and were tagged in both the Northwest branch (1/39 or 2.6 %) and the Southwest branch (2/9 or 22.2%). Two of these three repeat spawners that exited the river system in the spring of 2009 returned to spawn again as second time consecutive spawners in 2009, one from each branch. Four female salmon tagged in the spring of 2008 (8.9 %, 4/45 salmon not returning as consecutive spawners) returned in 2009 as 3SW alternate repeat spawners.

Of the kelts tagged in spring 2009, four returned as consecutive spawners (8.7 %) during that year's summer. These fish included one female salmon (4.3 %) from the Southwest branch and two female salmon and one male grilse (13 %) from the Northwest branch.

There were no significant differences when comparing biological characteristics (age, sex, length, weight, condition factor measured during tagging) or migratory ones (time and speed of travel of kelts through the estuary) between consecutive and alternate spawners that would help differentiate the two groups at the kelt stage. No significant differences were found ($p > 0.05$) between repeat spawners and non-repeats of 2008 and 2009 when the two spawning groups were compared for each biological and migratory characteristic.

Kelts migrating upstream through the estuary during both years also spent an unequal proportion of time in each section of the estuary ($X^2_{calculated}$ value > df = 2, $p = 0.05$; see Appendix 3a, b, c for details). Kelts returning to spawn for a consecutive year in 2008 (n = 3) spent the majority of the time they were in the study area within the inner bay (average 8 d, range 2 – 16.1 d) compared to the main branch (average 2 d, range 0.3 – 3.9 d) and Northwest (0.4 d) and Southwest branches (average 0.4 d, range 0.3 – 0.6 d). In 2009, repeat spawners from 2008 and 2009 (n = 9) spent most of their time in the inner bay (n = 6; average 1.3 d, range 0.5 – 4.4 d), the main branch (n = 1; 0.9 d), or the Northwest and Southwest branches (n = 2; average 0.9 d, range 0.6 – 1.3 d).

No tagged repeat spawning fish were documented in the estuary during the fall or winter monitoring periods. Once they had passed the head-of-tide units and entered the river system they remained there until survivors migrated back to the ocean in the following spring.

The three consecutive spawners that returned to the river system in 2008 took an average of 10.1 d (2.5 – 20.7 d) to reach the head-of-tide at an average speed of 13.8 km/d (3.3 – 27.1 km/d). The four consecutive spawners tagged in 2009 and returning the same year took an average of 1.7 d (1.1 – 2.1 d) at an average speed of 43.9 km/d (32.6 – 57.5 km/d) to reach the head-of-tide. Both consecutive and alternate spawners tagged in 2008 and returning in 2009 reached the head-of-tide in an average of 2.5 d (1.3 – 5.8 d) at an average speed of 36.7 km/d (11.8 – 51.4 km/d).

Synchronicity and passage

In 2008 and 2009, kelts exited the estuary system over a 20 day period (median exit date of May 24 and 25, range May 15 to June 3) and a 16 day period (median exit date May 18 and 19, range May 11 to May 26), respectively (Figure 2a). Dates of peak passage differed between years. In 2008, most kelts exited in three separate bouts of one to three days over a 14 day period. In 2009, the majority of kelts passed during a single concentrated time frame of four consecutive days. In 2008, the timing of the estuary exit for each kelt did not seem to be affected by the date of their release. Kelts from early and late releases were intermixed over the 20 day period as they exited the estuary (Table 1; Figure 2b). In 2009, kelts from early and late releases overlapped during their exit but showed a peak concentration of passage for each release (Table 1; Figure 2c).

The majority of the kelts that exited the estuary passed through the main center channel (Portage Channel). In 2008, 91.7 % (44/48) exited via the Portage Channel, 8.3

% (4/48) exited via the Neguac Channel (most northern exit) and none exited through Huckleberry Gully (most southern exit). In 2009, 89.1 % (41/46) exited through Portage Channel, 4.4 % (2/46) exited via the Neguac Channel and 6.5 % (3/46) exited through Huckleberry Gully. A higher percentage of kelts exited the estuary during the day compared to the night in both 2008 and 2009 (2008, 83.3 % day (40/48) versus 16.7 % night (8/48); 2009, 67.4 % day (31/46) versus 19.6 % night (9/46) and 13 % during the day and night (6/46)).

For the three repeat spawners that entered the estuary in 2008, each kelt passed through a different opening in the barrier islands, with two entering by day and one by night. When exiting the estuary in the spring of 2009, all three passed through Portage Channel, two during the day and one at night. In 2009, all five repeat spawners originally tagged in 2008 passed through Portage Channel during the day. The four consecutive spawners that were tagged in 2009 returned primarily through Portage Channel (n = 3), with one entering via Huckleberry Gully (n = 1). All these fish moved in during the day.

Depth of travel

The average detected depth for each kelt migrating though the estuary ranged between 0.8 and 6.5 m in 2008 (n = 19) and 0.5 and 5.6 m in 2009 (n = 7). Minimum and maximum depths that kelts frequented were 0 m (surface) and 19.4 m in 2008 and 0 and 7 m in 2009. Kelts returning in the summers of both years as consecutive spawners had average depths between 1.2 and 5 m (minimum 0 m, maximum 15 m; n = 4).

There was a great deal of variation in the depths of travel among individual kelts. In general, the largest numbers of detections for each individual were concentrated within a depth range of 1 to 4 m. However, depth records were either concentrated near the surface, or deeper in the water column. Of the 19 kelts with T/P tags that exited the estuary in 2008, 11 (57.9 %) had the majority of their detections documented between 0 and 2 m, 7 (36.8 %) between 3 and 5 m, and one kelt (5.3 %) between 6 and 7 m. In 2009, 2 (28.6 %), 3 (42.9 %), and 2 (28.6 %) of the seven kelts were between 0 - 1 m, 2

- 3 m, and 4 - 5 m, respectively. Kelts migrating upstream through the estuary (n = 4) had the majority of their detections documented between 0 - 2 m or 3 - 5 m.

Excursions to shallower and deeper depths within the water column were observed, depending on the kelt, generally, to deeper areas. Kelts that primarily traveled deeper within the water column rarely entered the top meter of water. The prevalence of diving varied among kelts in the estuary. In 2008, the percent of detections categorized as dives per kelt was between 0.4 and 32.8 %. In 2009, it was between 3.6 and 37.2 %. Returning kelts in both years had a dive percentage between 10 and 43.8 % of their total depth detections (Figure 3a, b).

Shallow and deep sites were compared to determine if diving was related to available depth ranges. The average depth of travel at shallow locations (Cassilis on the Northwest branch, 5 m deep at VR2 location; Doyals brook on the Southwest branch, 5 m deep at VR2 location) compared to the deeper location (Nordin on the main branch, 13 m deep at VR2 location) were similar in most circumstances, indicating that a same range of depths was frequented at both locations. Just over a quarter of the 19 kelts in 2008, one of the seven exiting in 2009 and one of the four returning back to the river over both years were detected at deeper depths at Nordin than were possible at Cassilis and Doyals Brook. For some individuals, the deeper depths were occupied short term and they mostly travelled near the surface. By contrast, other individuals remained mostly in deeper water when in the area of Nordin (Figure 4a, b, c).

Temperature and estuary conditions

Kelts exiting the estuary experienced temperatures averaging 11.3 °C in 2008 and 2009 (range 4.7 – 14.9 °C; 2008, range 8 – 15.1 °C; 2009). Repeat spawners that entered the estuary in summer experienced average temperatures of 18 °C (13.2 – 23.7 °C) in 2008 and 17.6 °C (12 – 19.8 °C) in 2009.

Measurements of temperature, dissolved oxygen and salinity within the Miramichi estuary showed only small gradual vertical changes for all three values. No significant differences were observed for these three characteristics throughout the system each year (Table 2). The presence of the salt wedge within the estuary began to appear between lower Beaubears Island and Nordin, depending on the tidal stage.

DISCUSSION

Survival

The high kelt survival from release to sea entry in both years (92 %) observed in this study is similar to that reported for kelts captured by angling from the LaHave River, Nova Scotia (90 %; Hubley et al. 2008) and the River Alta, Norway (92 %; Halttunen et al. 2009), but was higher than what was observed for the York River, Quebec (70 %; Hedger et al. 2009). These results indicate that estuary mortality for kelts is low and key mortality events occur in either the freshwater over-winter stage or during subsequent time spent at sea.

All fish tagged in this study were obtained from anglers during the spring salmon fishing season. The high rate of survival in this study indicates that catch-and-release fishing does not have a large impact on kelt mortality. This is consistent with previous work on the effects of catch-and-release fishing on kelts, which found no mortalities and a quick recovery time from angling (Brobbel et al. 1996; Whoriskey et al. 2000; Halttunen et al. 2010).

Of the six mortalities recorded in both years of this study, one was a large female salmon tagged on the Southwest branch in 2009. This kelt was not detected again after its release and the possible cause of death may have been associated with stress due to the surgical procedures. The causes of mortality for the remaining five kelts are speculative. The mortalities, particularly within the main branch where the salt wedge begins to appear, may have been affected by complications associated with re-acclimation to saline conditions (Handeland et al. 1998). Other environmental stressors and external factors (e.g., predation, angling) may also have influenced mortality.

While in this study, kelt mortality increased with distance traveled, sample sizes were too low to determine how sex, age and length related to survival. Mortality levels were very low, creating difficulty in determining the degree to which these variables affect kelt survival. However, these low levels suggest that the variables tested have few negative effects on kelt survival. Discounting the lone female salmon that may have died from post surgical complication, three males and two females died in the estuary. Jonsson et al. (1991b) reported that energy reserves in males are much lower than in females, so, surviving the winter and subsequently the spring migration may be more difficult for males. However, the almost equal proportion of mortalities for males and females suggest that age, sex and length did not have large effects upon survival through the estuary.

The lone mortality of the 11 first time repeat spawners via the aboriginal fishery indicates that once in the Miramichi estuary the rate of mortality is very low. Overwinter survival of the three female repeat spawner salmon in 2008 was also high (100 %). Females and salmon are believed to have higher energy reserves than males and grilse after spawning, which may aid them in surviving the winter (Jonsson et al. 1991b; Niemelä et al. 2000). Within North America winter survival of Atlantic salmon kelts is considered to be relatively high (Cunjak et al. 1998; Hubley et al. 2008). The Miramichi system has a large number of deep pools and backwaters as well as a tidal presence deep into the rivers where kelts have been documented to overwinter (Komadina-Douthwright et al. 1997). This apparently provides a favourable environment.

Time spent in the estuary

Kelts migrating through the estuary did not spend equal amounts of time in the upper, middle and lower sections, which is consistent with what has been observed for kelts from other rivers (Hubley et al. 2008; Hedger et al. 2009). Within the Miramichi, kelts spent the greatest amount of time in the upper sections (six to nine days; Northwest and Southwest branches) and less in the middle and lower sections (about one day; main branch and inner bay). This pattern is similar to that documented by Hedger et al. (2009) where kelts spent most of their time in the delta (~ 16 d) downstream of the river mouth. This contrasts with the results of Hubley et al. (2008), where kelts spent the majority of their time in the lower estuary (about five days). Possible reasons for this difference may be accounted for by site specific differences in each river system or that kelts in this study were tagged in the estuary and thus went through a period of recuperation and little activity in the upper reaches after release.

Within the upper sections of the estuary, kelts remained for longer periods of time in the area around their respective release sites and the first receiver downstream in each branch than in the remainder of the estuary downstream. These two downstream areas are short in length (1.11 km on the Northwest branch and 3.24 km on the Southwest branch). Kelts tagged in both years spent on average about the same amount of time in each short section. Prolonged periods of time spent in and around the release site may be due to the time needed to recuperate from the stresses associated with the capture and surgical procedures. However, Thorstad et al. (2000) found no effects of tagging on the swimming performance of farmed adult Atlantic salmon and negligible short term effects (reduced feeding and initial weight loss) were also found on the behaviour of tagged Atlantic salmon smolts held for observation in the laboratory (Lacroix et al. 2004), indicating that effects of tagging are negligible.

The delay may alternatively be due to feeding. A large population of rainbow smelt migrates up the Miramichi River system (Chaput 1995) through the release area during the time when the kelts were captured, tagged and released. Kelts feed heavily during their initial migration in order to regain lost energy reserves (Cunjak et al. 1998; Hubley et al. 2008). It is possible that kelts remained in the small release area to feed heavily on smelt before undertaking the rest of their migration. Early feeding was hypothesised by Hedger et al. (2009) to be the cause of observed prolonged stay in the York River delta. Komadina-Douthwright et al. (1997) also documented upstream movements of kelts around the head of tide area of the Northwest branch of the Miramichi River. These movements were associated with smelt moving upstream in spring.

The average time kelts spent in the upper sections (Northwest and Southwest branches) was greater than in the rest of the estuary. This may indicate prolonged feeding in this area; acclimation is not an issue due to the lack of saline conditions in the upper sections.

The three repeat spawners tagged in spring 2008 that exited the estuary in spring 2009 after overwintering traveled at similar speeds from the detection on the first receiver to the exit as kelts that were tagged in spring 2009. Due to the recovery from tagging, it was thought that kelts tagged in 2009 may remain in the estuary longer and travel more slowly once detected at the first receiver than the exiting repeat spawners tagged in 2008. Halttunen et al. (2010) reported an initial delay in migration in the river system after release for kelts that were angled and tagged recently versus those tagged many months earlier. No differences were documented in this study between recently and non-recently tagged kelts, suggesting that once kelts have reached the first receiver and the onset of migration has occurred for kelts tagged in 2009, the effects of tagging are no longer an issue. Past this point, feeding, acclimation to salt water and direction of travel (moving upstream) may regulate migration time and speed and not the effects of tagging.

Occasional movements by kelts (n = 4 in 2008, n = 12 in 2009) into the opposite branch (Northwest or Southwest) from the branch they were released into were documented. These excursions were of relatively short distance (< 5 km) and time (< 1 d) before downstream movements were continued. These back and forth movements have been documented in kelts (Hubley et al. 2008; Hedger et al. 2009) and are similar to those of bright salmon traveling with the prevailing tide within the Miramichi estuary (Stasko 1975). It is possible that kelts migrating through the estuary are either moving periodically with the tidal currents or following prey such as smelt upstream.

Travel time and speed

The time it took kelts to exit the estuary when measured from their release was twice as long as when it was measured from the first reading on the first receiver. This large difference in travel time and speed supports earlier findings in this study that kelts remain in the upper reaches to recuperate and/or feed. Average speeds of travel from the first receiver to estuary exit in both years (14.5 km/d, 2008; 21 km/d, 2009) were faster than those reported by Hedger et al. (2009; at 12 km/d) and Hubley et al. (2008; < 10 km/d). Only kelts traveling through the Alta Fjord have been reported to move faster than the Miramichi fish (38.4 km/d; Halttunen et al. 2009).

Speeds of travel increased as kelts progressed downstream through the estuary, similar to what was observed by Hedger et al. (2009) in the York estuary, and in the bay area of the LaHave River (Hubley et al. 2008). By contrast, Halttunen et al. (2009) found kelt speeds decreased along the estuary of the Alta River toward the sea. The differences observed in the Alta River from the Miramichi may be due to a lower abundance of forage items near the head of tide region and a greater abundance further into the estuary fjord system or the need to acclimate to the increase in salt concentration within the fjord once they have exited the estuary. The Alta estuarine and fjord system is larger and more open creating a semi enclosed system where kelts may spend more time beginning to recondition prior to entering the open ocean. The increase in speed and decrease in time within each area recorded in this study may be due to a decrease in the feeding opportunity and need for acclimation time to salinity as they progressed to the ocean.

Repeat spawners

The percent of repeat spawners from fish tagged in 2008 (14.6 %) and 2009 (12.2 %) falls within estimated rates for the Miramichi River system as a whole (Chaput and Jones 2006; Chaput et al. 2010). The number of consecutive spawners returning to this system has increased since 1995 and has been associated with the increase in prey fish biomass in the Gulf of St. Lawrence (ICES 2008b; Chaput et al. 2010). Our observed return rates have been high for large salmon at 24 % (7/29) in 2008 and 71.4 % (5/7) in 2009, and low for grilse (0 and 2.4 % respectively, in 2008 and 2009). Using the biological and migratory characteristics we recorded, we were unable to distinguish if a certain grouping of kelts would be alternate or consecutive spawners or to find any differences between those that returned and those that did not. It has been suggested that consecutive and alternate spawner returns are regulated by fish size at maturity. Smaller 1SW and 2SW fish thus become consecutive spawners and larger ones alternate spawners (Jonsson et al. 1991a). The lack of returning repeat spawners from our tagged grilse kelts, and the absence of significant differences in length of consecutive and alternate spawners does not support this hypothesis, at least for the Miramichi population. For our fish that female salmon (maiden and repeat) were more often repeat spawners than were male salmon, or male and female grilse. This higher return rate of female salmon has also been documented in previous studies (Ducharme 1969, O’Connell et al. 2006) in North America.

Returning repeat spawners spent a greater amount of time in the inner bay (lower section) than in the middle and upper sections of the estuary. This may be due to the initial amount of time needed to acclimate to lower saline conditions in the estuary (e.g. Stasko 1975). We found that once the bright salmon had entered the river system, they did not venture into the estuary again until the following spring during their migration to the ocean. Kelts have been documented to overwinter within the vicinity of the estuary of the Miramichi River system, where tidal movements are still present (Komadina-Douthwright et al. 1997). In this study, fall and winter movements were not documented in the monitored area.

Repeat consecutive spawners returning to the river system in 2008 took considerably longer (~ 10 d; 13.8 km/d) to reach the head-of-tide than the 2009 consecutive and alternate spawners (1.7 d, 43.9 km/d and 2.5 d, 36.7 km/d respectively). In all cases, travel speeds were greater than those observed by Hubley et al. (2008) where the single kelt they observed traveled upstream more slowly than when it left in spring. One study on bright salmon migration conducted in the Miramichi estuary reported speeds of 1.44 km/d (Elson et al. 1972), which is at the lower range of those observed in this study.

The large difference in speeds of travel between returns in 2008 and 2009 may be due to differences in estuarine temperatures between the two years. In 2008, repeat spawners came back between the middle of July and August when waters were warmer, while in 2009 they returned earlier, in May to July, when water temperatures were cooler (average temperature at mouth of estuary 18.1 °C and 16.6 °C, in 2008 and 2009 return periods respectively; average temperature in the Northwest branch 20.4 °C and 16.9 °C, respectively and Southwest branch 21.5 °C and 17.6 °C, respectively).

Synchronicity and passage

The pattern of passage through the estuary exits differed between 2008 and 2009. In 2008, kelts exited the estuary over a longer period of time, with multiple exit peaks. In 2009, passage was shorter and there was only one period of peak passage (Figure 2a). The cause of the differing patterns of passage may be biological (time spent recuperating, feeding) or environmental (water cues triggering downstream movement) that may vary temporally and with each kelt. The dephasement of exit dates did not match those of the release dates, indicating that kelts do not travel in fixed groups within the estuary. Individual kelts tended to “leap frog” one another during migration (Figure 2b, c).

Exit from the estuary into the Gulf was mostly through Portage Channel in both years; the deepest and widest of the estuary's three exits. The same choice was seen among returning repeat spawners entering the system. When a choice of exit was present, Hedger et al. (2009) found kelts leaving a system used the exit with greater currents and salinity concentrations. It may also be that returning bright salmon are attracted to greater currents and indications of lower salinity or concentrated olfactory cues. While exiting and entering the system, kelts passed between the barrier islands during the day 77.1 % of the time over the two years, similar to the findings of Hedger et al. (2009). This perhaps reflects low potential predation pressure by grey seals in the area (Hammill and Stenson 2002) that could cause salmon to travel at night to avoid mortality.

Depth of travel

The average depths of travel for kelts during both years were generally shallow with high variability, but highlight the fact that individual kelts are depth-specific. Individual kelts remained in a narrow depth range of one to four meters within the water column. We documented three main depth trajectories in our study: travel near the surface, travel at depth (> 3 m) rarely moving towards the surface and travel throughout the water column. The majority of kelts traveled within the top two meters (57.9 %) in 2008 and the top three meters (71.5 %) in 2009. This is deeper than depths of travel recorded by Hubley et al. (2008).

Vertical movements for individuals within the estuary outside their zones of concentration were mostly deeper and rarely towards the surface. Dive percentage from both years for shallow and deep dives per kelt varied between 0.4 and 37.2 %. Similar to what was observed by Hubley et al. (2008), repeat spawners returning in summer dove more (10 – 43.8 % of individuals diving) than kelts leaving in spring. This may be due to warmer surface temperatures during summer. The cause of these dives during spring may be linked to orientation and acclimation to an increase in salt concentrations as they migrate to the ocean and to foraging for prey items within the water column (Hubley et al. 2008; Halttunen et al. 2009).

Diving behaviours by most kelts did not seem to be regulated by water depth. Only 7/30 kelts over both years frequented near maximum depths at a deep site (Nordin) that were deeper than the shallow sites at Cassilis and Doyals Brook. The depth of the water column regulates the maximum depth a kelt can attain, but a kelt will not necessarily use that available depth. In some cases kelts traveled more deeply in the shallow areas than in the deeper area, suggesting that depth of travel does not only depend on availability.

Temperature and estuary conditions

Temperature variation experienced by kelts throughout the estuary in spring and summer is most likely linked to the various diving patterns that were documented for each kelt as slightly cooler temperatures were found deeper in the water column (unpublished data). Unfortunately, individual data records are too limited for more extensive analysis.

The estuary as a whole is well mixed, having a narrow but gradual change in temperature, dissolved oxygen and salinity values from the head-of-tide to the exit and from the surface to the bottom. The relatively small variations of these values in the estuary in spring provide a consistent change in the environmental conditions for kelts to adapt to during migration. The lack of abrupt changes may place less physiological stress upon kelts and repeat spawners exiting and entering the Miramichi River system during this time.

CONCLUSION

There was high survival of kelts exiting the Miramichi estuary. This points to high mortality in reconditioning adults within the Gulf of St. Lawrence or the Atlantic Ocean, as adult returns to the river system remain low. There has been an extensive effort to increase the number of salmon returning to the river systems. The implementation of catch-and-release has been an effective management tool for increasing repeat spawners. We used angled fish in our study, and their high rate of survival and return indicate that the effects of catch-and-release fishing was negligible.

Kelts spent a large amount of time within the first sections of the estuary around the head-of-tide area, possibly feeding heavily on baitfish or recuperating from the stresses of surgery. In the Miramichi system, the initial stage of estuary entry may prove to be important in the kelt gaining enough energy to ensure survival during the first stages of migration and may play an important role in later survival and their return to the river system. Further research is needed to determine if there are differences in survival rates or migratory timing based on when kelts have exited the river system (early or late).

There was also a higher rate of consecutive spawners than alternate ones, consisting of a greater number of female MSW salmon. Due to the importance of these spawners in contributing to the spawning class of a given year, more research is needed to determine what differentiates the two spawning groups and where these fish go once they are out of the river system.

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Table 1: The median exit date(s) and range for kelts exiting the Miramichi estuary by each release group of kelts tagged in 2008 and 2009 at the Miramichi estuary heads of tides.

Release date	Median (range)
May 7 2008	May 24, 25 (May 16 – June 3)
May 8 2008	May 16 (May 15 – 17)
May 9 2008	May 27 (May 16 – June 7)
May 13 2008	May 25 (May 18 – June 1)
May 14 2008	May 25, 26 (May 19 – June 1)
May 6 2009	May 14, 15 (May 11 – 18)
May 7 2009	May 16 (May 12 – 20)
May 8 2009	May 19 (May 12 – 26)

Table 2: The range in temperature, dissolved oxygen and salinity measured throughout the Miramichi estuary from the head-of-tide to the Barrier Islands in May 2008 and 2009.

Parameter	Range	
	2008	2009
Temperature (°C)	8.3 – 12.3	6.7 – 13.6
Dissolved Oxygen (% saturation)	90 – 121.7	87.3 – 102.9
Salinity (ppt)	0 – 23.7	0 – 25.6

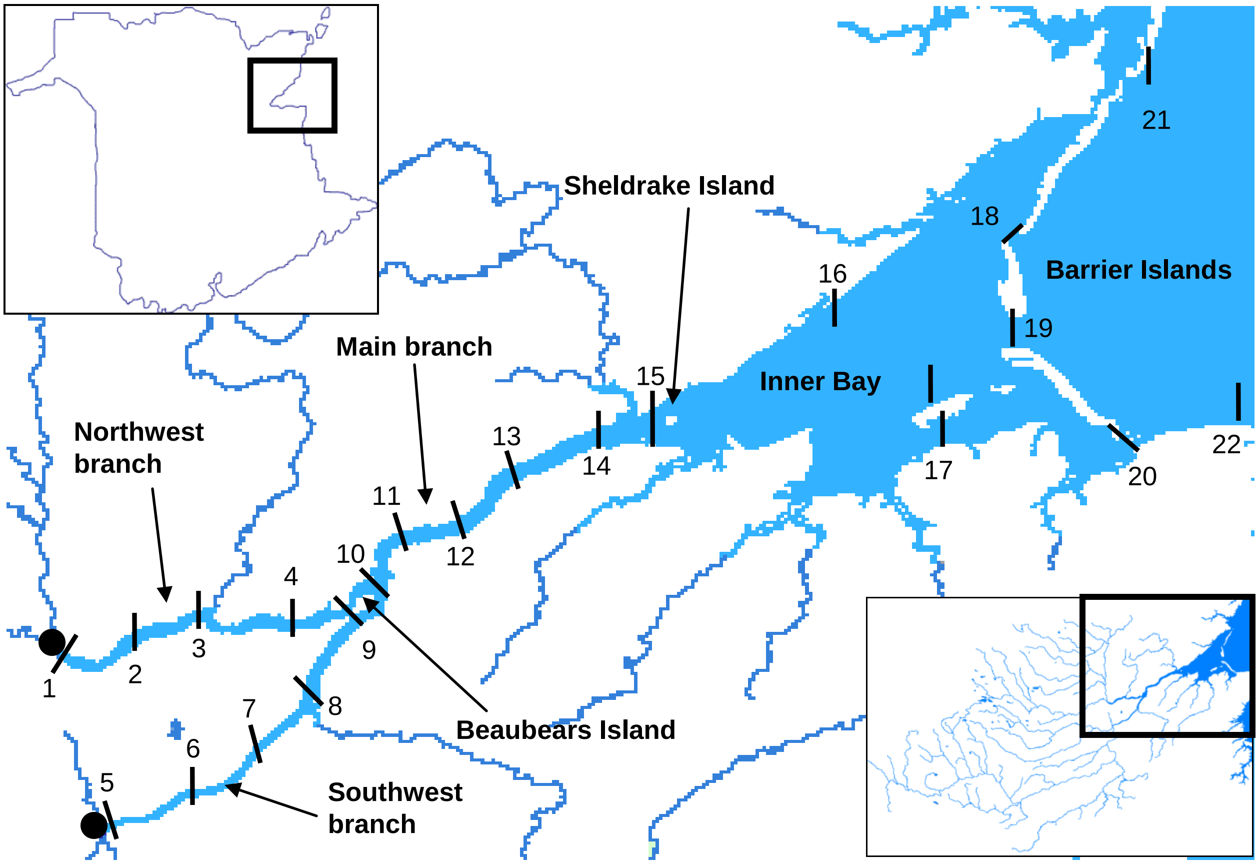
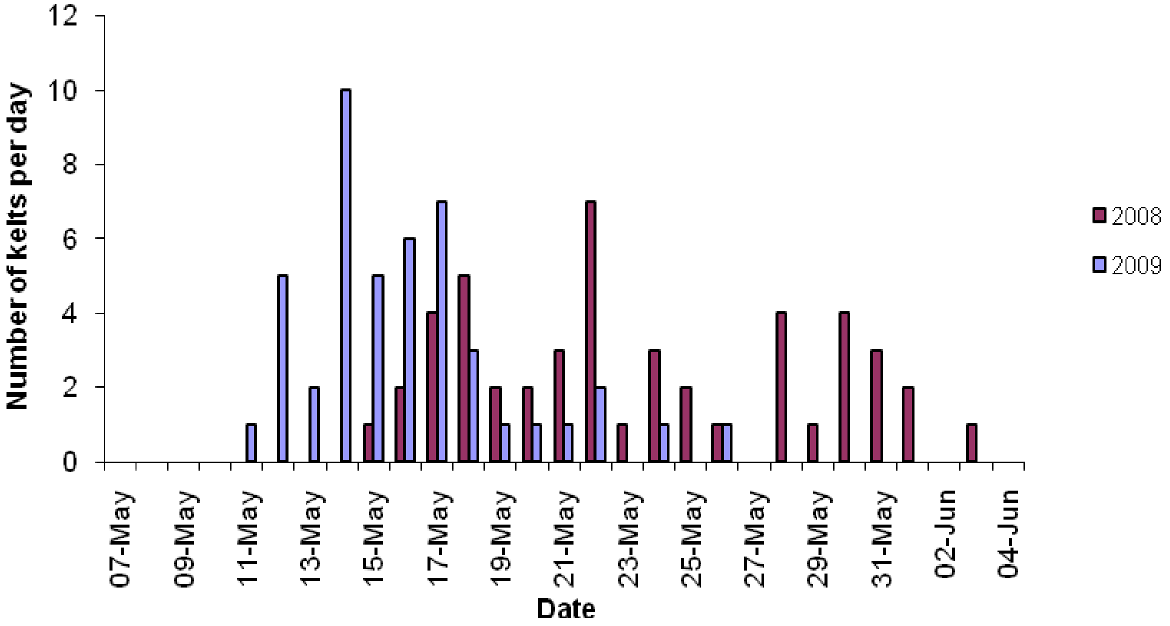
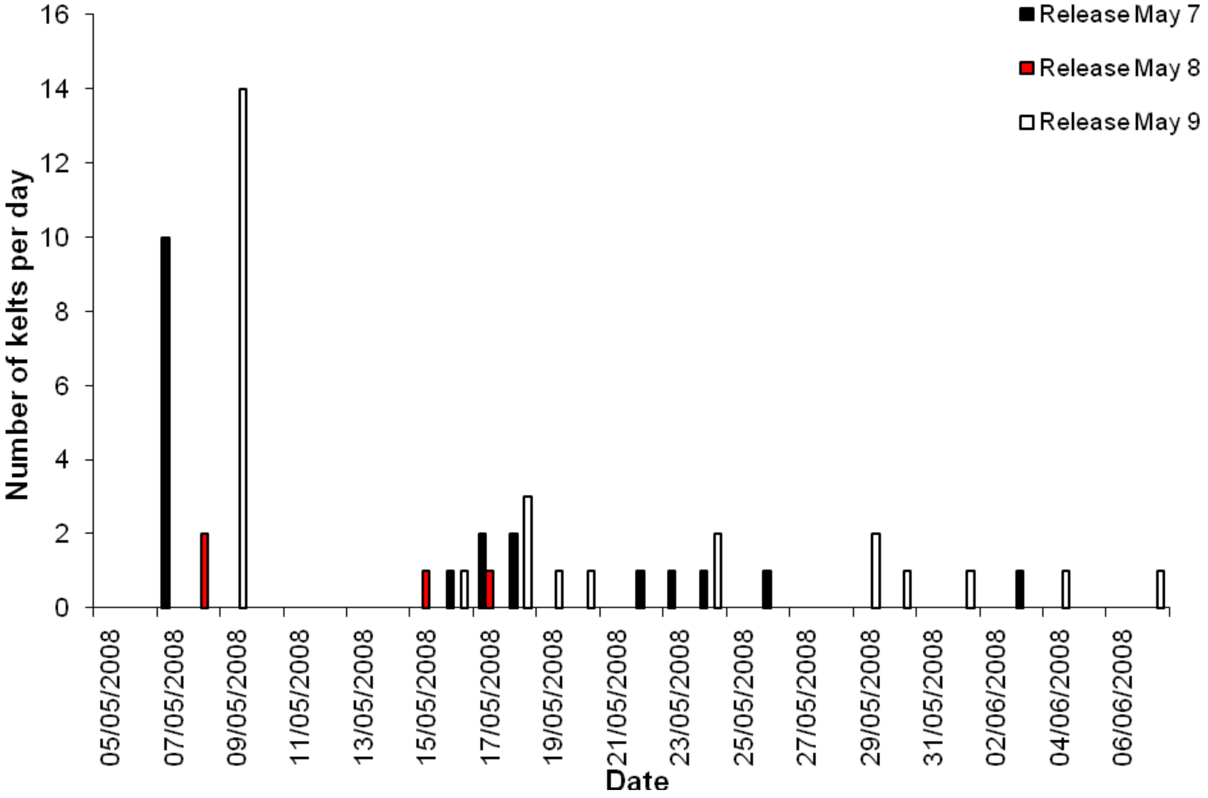


Figure 1: The Miramichi estuary depicting the head-of-tide release locations (Circles) and VR2 placements (Black lines). 1) Sutherland Brook, 2) Cassilis, 3) Millstream, 4) Eel Ground, 5) Quarryville, 6) Doyals Brook, 7) Millerton, 8) Barnaby Island, 9) Upper Beaubears Island, 10) Lower Beaubears Island, 11) Nordin, 12) Douglasstown, 13) Middle Island, 14) Bartibog River, 15) Sheldrake Island, 16) North Shore of Inner Bay, 17) Bay du Vin Island, 18) Neguac Channel, 19) Portage Channel, 20) Huckleberry Gully, 21) Tabusintac, 22) Escuminac Point. Environmental monitoring locations were at VR2 locations 1 – 15 and 18 – 20 each year.



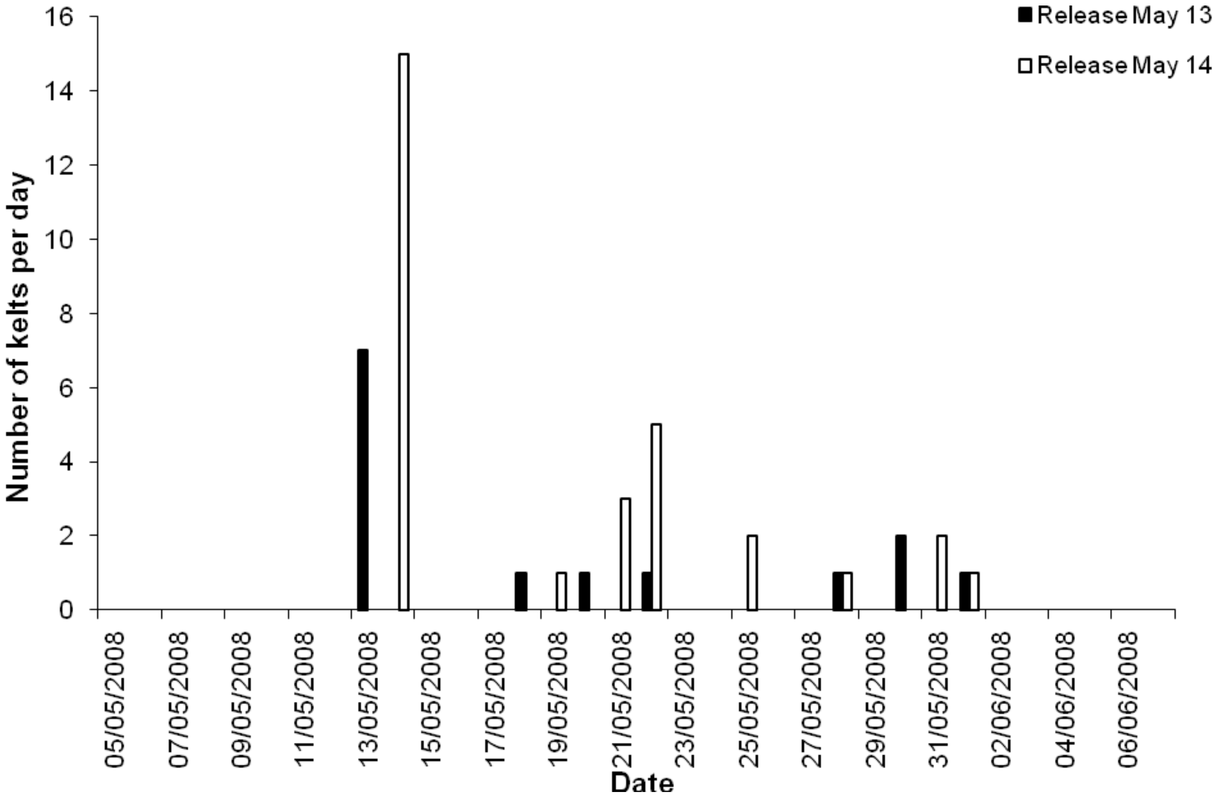
Number of kelts per day
0
2
4
6
8
10
12
07-May
09-May
11-May
13-May
15-May
17-May
19-May
21-May
23-May
25-May
27-May
29-May
31-May
02-Jun
04-Jun
Date
2008
2009

a)



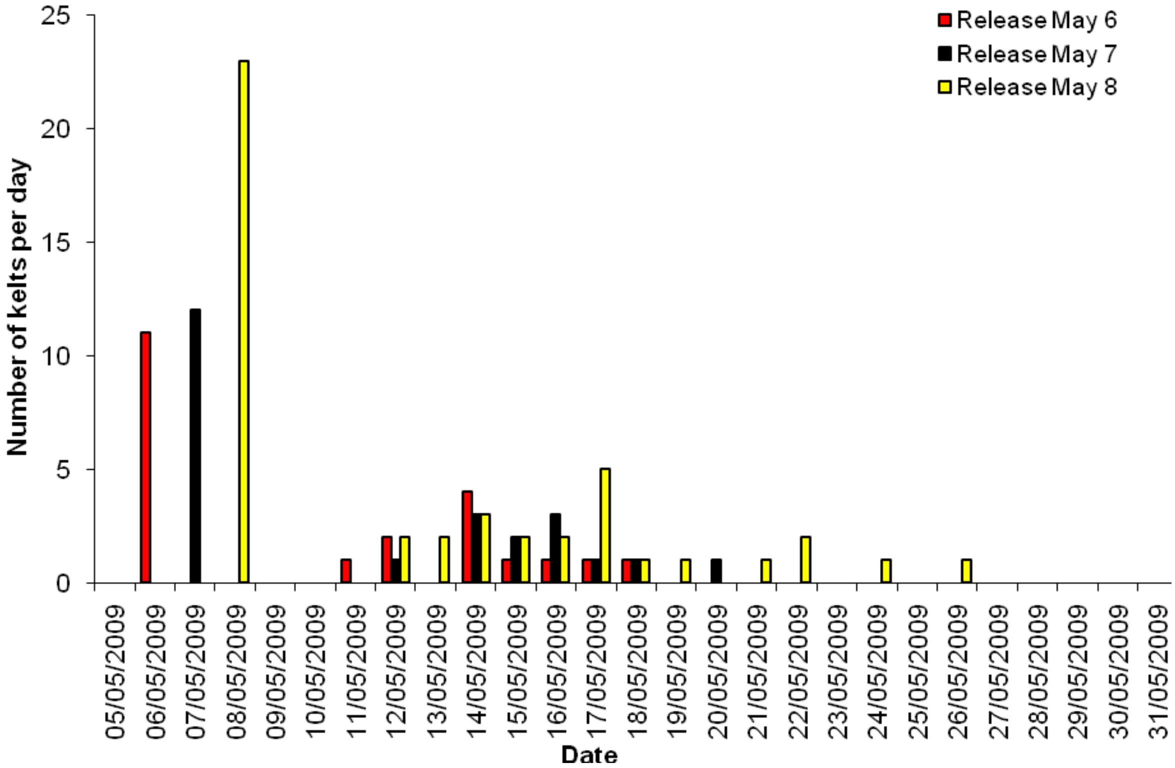
Number of kelts per day
0
2
4
6
8
10
12
14
16
05/05/2008
07/05/2008
09/05/2008
11/05/2008
13/05/2008
15/05/2008
17/05/2008
19/05/2008
21/05/2008
23/05/2008
25/05/2008
27/05/2008
29/05/2008
31/05/2008
02/06/2008
04/06/2008
06/06/2008
Date
Release May 7
Release May 8
Release May 9

b)



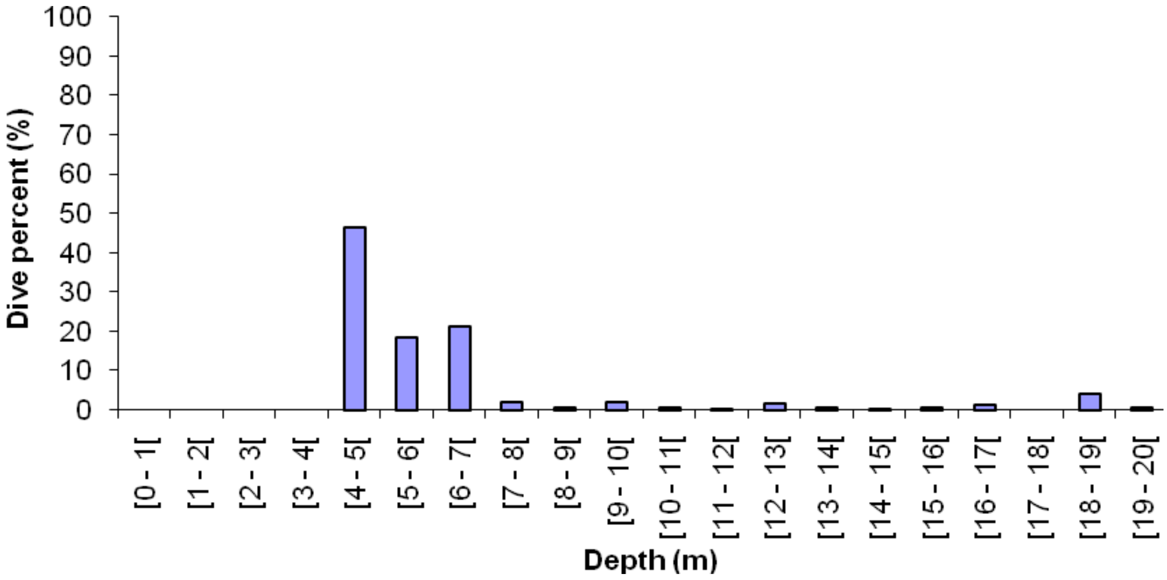
■ Release May 13
□ Release May 14
Number of kelts per day
0
2
4
6
8
10
12
14
16
Date
05/05/2008
07/05/2008
09/05/2008
11/05/2008
13/05/2008
15/05/2008
17/05/2008
19/05/2008
21/05/2008
23/05/2008
25/05/2008
27/05/2008
29/05/2008
31/05/2008
02/06/2008
04/06/2008
06/06/2008

c)

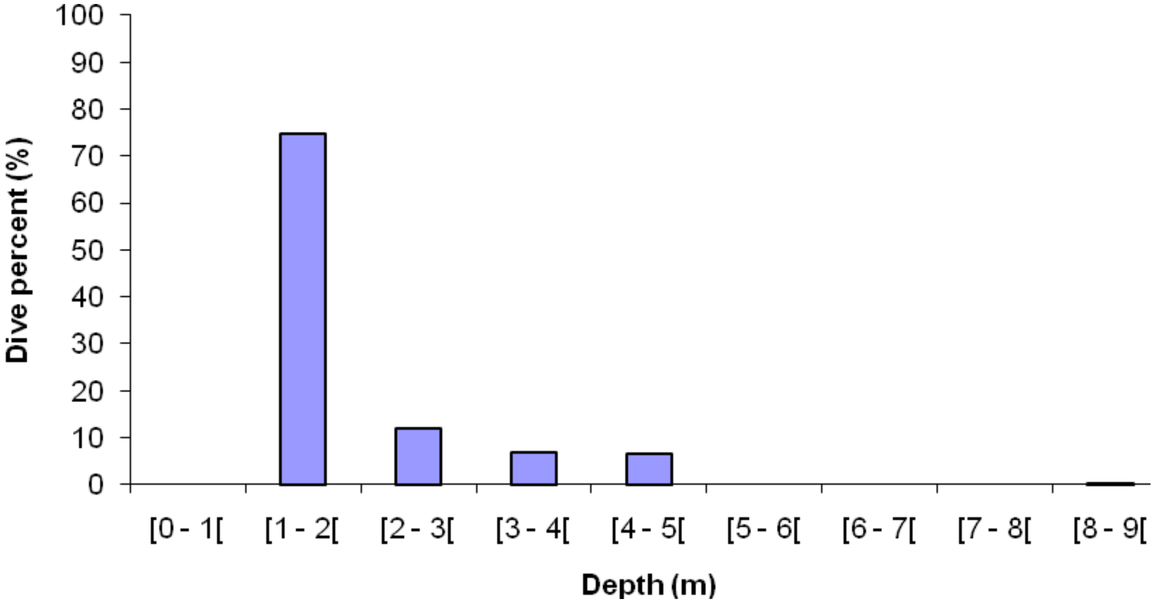


d)

Figure 2: a) The number of kelts that exited the Miramichi estuary on the given days in 2008 and 2009. b) The number of kelts that exited the Miramichi estuary on given days in 2008 from releases on May 7, 8 and 9. c) The number of kelts that exited the Miramichi estuary on given days in 2008 from releases on May 13 and 14. d) The number of kelts that exited the Miramichi estuary on given days in 2009 from releases on May 6, 7 and 8.

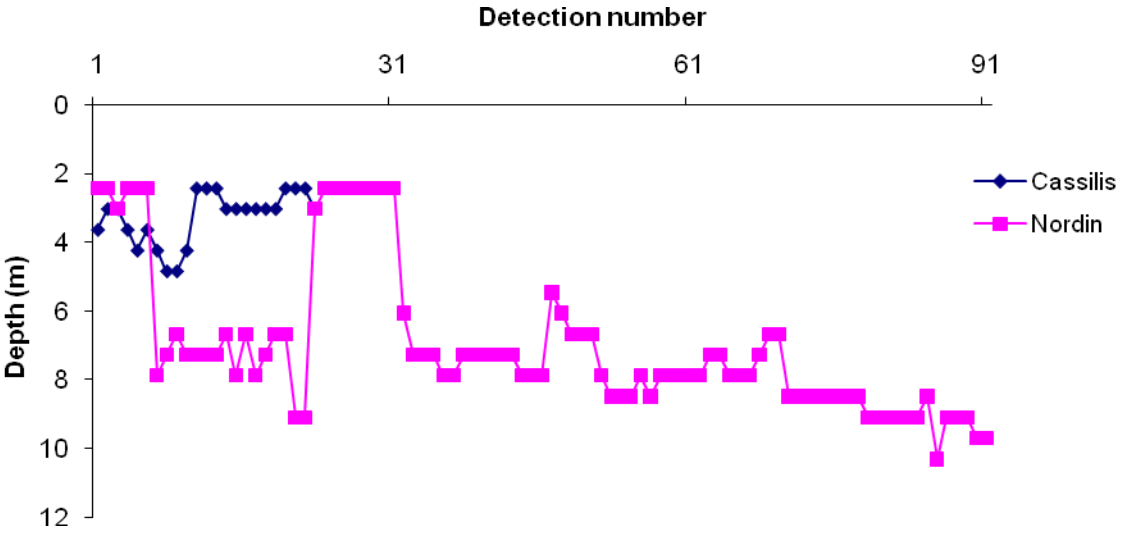


a)

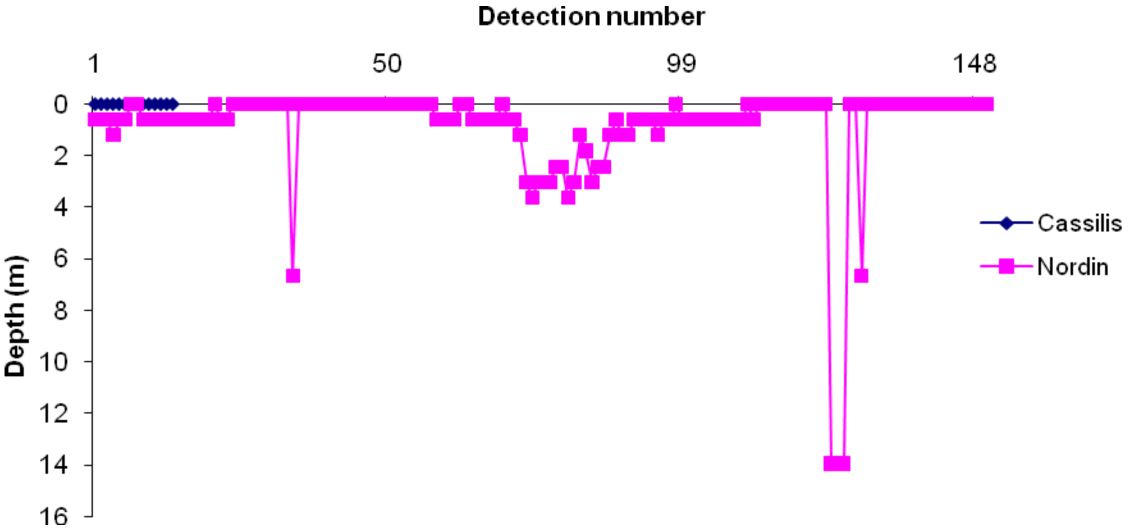


b)

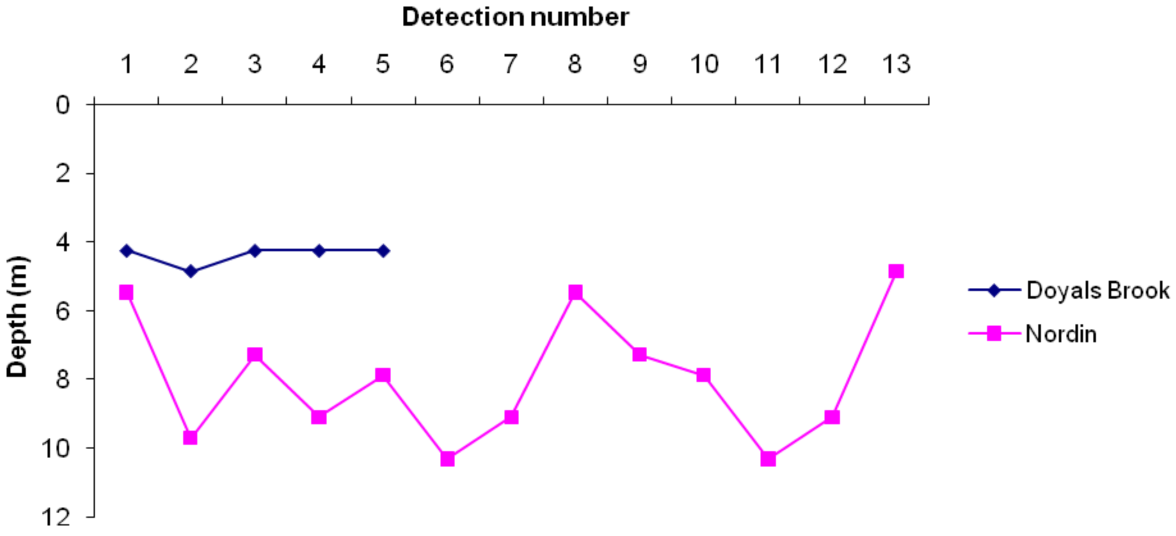
Figure 3: a) The percent of detections categorized as dives for kelt ID 13541. b) The percent of detections categorized as dives for kelt ID 13551.


Detection number
1
31
61
91
0
2
4
6
8
10
12
Depth (m)
Cassilis
Nordin

a)


Detection number
1
50
99
148
0
2
4
6
8
10
12
14
16
Depth (m)
Cassilis
Nordin

b)



c)

Figure 4: a) The depth profile of kelt (ID 13545) a shallow site on the Northwest branch (Cassilis – 5 m deep) and a deep site on the main branch (Nordin – 13 m deep). b) The depth profile of kelt (ID 13547) at a shallow site on the Northwest branch (Cassilis – 5 m deep) and a deep site on the main branch (Nordin – 13 m deep). c) The depth profile of kelt (ID 13553) at a shallow site on the Southwest branch (Doyals Brook – 5 m deep) and a deep site on the main branch (Nordin – 13 m deep).

CONNECTING STATEMENT

Chapter 2 examined the migration and survival of kelts leaving the estuary system, documented the environmental conditions kelts experience during estuary migration and the potential impacts of catch-and-release fishing. Chapter 3 examines the kelts’ migratory progression along the Atlantic Ocean coastline through the Gulf of St. Lawrence once they have left the Miramichi system, and infers migratory pathways of different age classes of kelts.

CHAPTER 3: THE MIGRATORY MOVEMENTS OF MIRAMICHI ATLANTIC SALMON KELTS WITHIN THE GULF OF ST. LAWRENCE AND ATLANTIC OCEAN COASTLINE

ABSTRACT

Atlantic salmon kelts from the Miramichi River (n = 94 of 100 tagged) were monitored with acoustic telemetry receivers placed along the coast of the Gulf of St. Lawrence (Gulf), Atlantic Ocean and through the Strait of Belle Isle in 2008 and 2009. Once in the Gulf, kelts were occasionally detected along the coast line during migration. Kelts were documented exiting the Gulf via the Strait of Belle Isle (22 in 2008, 9 in 2009) over a short time frame of 20 d in 2008 and 35 d in 2009. Speeds of travel for kelts within the Atlantic Ocean ranged from 10.4 km/d to 69.9 km/d. Repeat spawners, returning as consecutives in 2008 and 2009, did so between 44 and 64.8 d and as alternates in an average of 394.7 d after exiting the Miramichi system. There are indications from the travel speeds that consecutive spawners may be exiting the Gulf to recondition. Alternate spawners may enter coastal zones long distances from their natal river during their return migration, possibly in search of their natal river. The oceanic migration of kelts is important to understand as subgroups based on age, sex or spawning group may frequent separate areas.

INTRODUCTION

The number of Atlantic salmon (*Salmo salar*) returning to North American rivers has declined over the last three decades. Management measures taken in both fresh water and at sea have failed to reverse the decline (ICES, 2009). Different hypotheses have been proposed regarding the causes of the decline (Friedland *et al*., 1998; Friedland *et al*., 2000; Cairns, 2001). It is likely that a mix of factors acting individually and in concert, have contributed. Current research indicates that the principal causes are most likely occurring within the marine environment (Anderson *et al*., 2000).

Atlantic salmon are iteroperous, and some individuals spawn repeatedly during their life span (Mills, 1989; Scott & Crossman, 1998). The repeat spawner component of adult salmon returns to North American rivers has become increasingly important for insuring the conservation and resilience of Atlantic salmon populations (Chaput *et al*., 2010). Hence knowledge of the movements and habitats used in the ocean by the fraction of the population that returns to sea after a first spawning, and which survives to return for subsequent spawning, is important.

Atlantic salmon that have survived spawning are termed kelts. Kelts are energetically-depleted, and return to the sea in late fall or early spring for additional growth and to recondition by feeding on the abundant prey items. This aids in the preparation of kelts for future spawning (Jonsson *et al*., 1991b; Niemelä *et al*., 2000; O'Connell *et al*., 2006). These repeat spawners may be either consecutive (spawn every year) or alternate (skip one or more years between successive spawnings) spawners. A given individual may alternate between the consecutive and alternate patterns of reproduction over its lifetime (Jonsson *et al*., 1991a; Niemelä *et al*., 2000; O'Connell *et al*., 2006). Repeat spawners are important because the larger repeat spawning females supply more eggs than smaller maiden individuals to the spawning class of a given year (Niemelä *et al*., 2006; Chaput *et al*., 2010), they contribute to maintaining genetic diversity (Ducharme, 1969) and serve as potential safeguards against population crashes at sea and repeated reproductive failure (Ducharme, 1969; Niemelä *et al*., 2000).

Research on kelts in general is lacking, and studies of their movement at sea are rare. Some work has examined kelt displacements within coastal zones (Hubley *et al*., 2008; Halttunen *et al*., 2009; Reddin *et al*., 2004), however, there has been little research on kelts outside of coastal marine habitats (Lagueux, 1953; Hedger *et al*., 2009). Away from the coastal habitats, our knowledge of Atlantic salmon feeding grounds is of a general nature. Specific feeding areas are population dependant, but to witch extent (geographical, watershed or river dependant) is not known. Known feeding grounds include the Labrador Sea, Grand Banks and the Bay of Fundy in the west Atlantic Ocean and the Norwegian, Barents and Baltic Seas in the East Atlantic (Templeman, 1968; Reddin, 1985; WWF, 2001). In general, populations originating from rivers in the West and East Atlantic remain in the feeding areas associated with each region (WWF, 2001). However, intermixing does occur at a presently unknown proportion.

The putative migration routes used by Atlantic salmon between the Gulf of St. Lawrence and the Atlantic Ocean feeding grounds are the Strait of Belle Isle and Cabot Strait (ICES, 2008a). Salmon migrating from south of the Gulf of St. Lawrence are believed to travel around Newfoundland to the Grand Banks and Labrador Sea areas (WWF, 2001).

In this project acoustic telemetry was used to document the coastal and Gulf of St. Lawrence movements of Miramichi River Atlantic salmon kelts during their post-spawning exit and subsequent return migration from the sea. The main objective of this study was to document their coastal and ocean migration routes and characteristics such as travel times and speeds.

METHODS

Study site

The Miramichi estuary covers an area of 300 km^2 (Figure 1). Tidal effects are evident up to 80 km upstream. There are three barrier islands in the mouth of the estuary, providing a limited number of channels through which fish can move into the Gulf of St. Lawrence (Robichaud-LeBlanc *et al*., 1998).

The Gulf of St. Lawrence covers approximately 200 000 km^2 and connects to the Atlantic Ocean in the south via either Cabot Strait (on average 104 km wide, 480 m deep) or in the north by the Strait of Belle Isle (on average 16 km wide, 60 m deep). The principal sub-surface feature of the Gulf is the Laurentian Channel, which begins near the Saguenay River and runs through Cabot Strait. Shallower waters are present to its north and south. Fresh water from the St. Lawrence River and salt water from the Atlantic Ocean entering the two straits create a cyclonic (counterclockwise) circulation of surface waters. These surface waters flow out along the southern coast and in along the northern coast (Fuentes-Yaco *et al*., 1997; Figure 1).

Hydrophone deployment

Hydrophones (Model VR2: single channel monitoring receivers manufactured by Amirix/Vemco, Halifax, NS) were moored at different positions within the estuarine portion of the Miramichi River from the head of tide to the Outer Miramichi Bay area. The receivers at a given position were placed to provide complete detection coverage of the channels that fish could pass through. Thus quantitative estimates of the numbers of fish surviving to each point could be calculated. Receivers were positioned as soon after ice breakup as feasible. The VR2's were placed from April 24 to May 10, 2008 throughout the Miramichi estuary starting at the head of tide area of each branch (Northwest (NW), Sutherland Brook; Southwest (SW), Quarryville) to the Barrier Islands and along the outer Miramichi bay area (Figure 1). The units in the inner and outer bay areas were removed between August 14 and 19, 2008. The receivers remaining in the estuary between the two heads of tide and Sheldrake Island were removed on October 6 and 7, 2008.

A total of 12 units were placed in the estuary on October 6 and 7, 2008, before the summer units were removed, to overwinter until spring 2009. These were suspended on a buoy in the water column about 1 m above the anchor on the river bottom. This minimized the probability of the unit being covered by bedload sediments, being snagged by floating debris, or having its float encased in winter surface ice. Receivers were placed near the locations of the summer units from Red Bank and Millerton in the Northwest and Southwest branches respectively to the Bartibog River within the main branch. Overwintering units were retrieved between April 24 and August 30, 2009.

Twelve units were re-deployed on August 4 and 5, 2009 for the fall monitoring period at the same locations as the 2008/2009 overwintering units in 2008. Thus, receiver coverage in the estuary was continuous for the duration of the study.

Spring and summer receivers were then deployed from April 24 to May 13, 2009 (n = 39) in the same locations as those in 2008. Units were placed prior to the removal of the 2009/2009 overwintering units.

Within 100 km along the coast to the north and south of the Miramichi River estuary exit to the ocean, Canada's Department of Fisheries and Oceans deployed a total of eleven (2008) and seven (2009) receivers in coastal areas to track striped bass (*Morone saxatilis*). We benefited from opportunistic detections of our fish on these receivers, although they were not positioned to provide quantitative estimates of fish arriving at this point.

About 110 km to the north of Miramichi Bay, 29 receivers were placed by the Atlantic Salmon Federation each year across Chaleur Bay (≈ 900 m apart) during the summers of 2008 (May 31) and 2009 (May 21) between Grand Anse, New Brunswick and Paspebiac, Quebec, This provided complete coverage of any tagged kelts that might enter this area.

About 800 km North of Miramichi Bay, twenty two receivers were deployed annually (≈ 800 m apart) during the summers of 2008 (June 20) and 2009 (June 18) across the Strait of Belle Isle between Green Island Cove (Newfoundland) and L'Anse au Loup (Labrador). This Strait is the Northern exit from the Gulf of St. Lawrence to the Atlantic Ocean.

Finally, we also benefited from limited deployments of receivers by colleagues from Memorial University of Newfoundland and DFO in Gilbert Bay, Labrador (n = 3; Labrador) and Trinity Bay, Newfoundland (n = 3; Newfoundland) (see Figure 1).

Kelt capture

All fished used in this study were captured by anglers fly fishing for kelts (single barbless hook) in a designated spring season for this activity. Anglers were not supervised by our biological team during their fishing, but notified us by sight, radio or cell phone of captures of fish that they were willing to provide us. We then pick up the fish in a boat equipped with a holding tank filled with fresh river water, and moved them back to our surgical site. Here, kelts were moved to a large aerated Xactic tank filled with fresh river water to recuperate from the stresses induced by angling for 15 to 20 minutes.

Kelt tagging

The surgical implantation of acoustic tags into the kelts took place near the head of tide on both the Northwest (Red Bank bridge) and Southwest (Quarryville bridge) branches of the Miramichi Estuary. Fifty kelts were tagged in each of 2008 and 2009.

Different tag models were used, depending on our resources, fish size, and our objectives. All tags were coded with a unique individual ID. In 2008, 20 V13's (13 mm in diameter, 36 mm long, 6 g in water) and 10 V16's (16 mm in diameter, 96 mm long, 16 g in water) that emitted an ID only, were deployed. In addition, in 2008 20 V16 tags with an ID and temperature and pressure sensor (T/P) were also used. These tags were distributed among fish captured in the two branches of the river, with 20 V13's, nine coded V16's and 12 coded T/P V16's placed on fish in the Northwest branch. The Southwest branch had no fish tagged with V13's, one fish with a V16 tag and eight individuals marked with T/P V16 tags. In 2009, 50 V16 tags (45 ID only, and five with ID and T/P readers) were used. A total of 22 tags with ID only and three coded T/P tags were implanted into fish from the Northwest branch. In the Southwest branch, 23 kelts were tagged with ID only tags and two with T/P tags (see Appendix 1a, b).

Tagging on the Northwest branch took place on May 7 (n = 11), May 9 (n = 14) and May 14 (n = 16), 2008. Tagging on the Southwest branch took place on May 8 (n = 2) and May 13 (n = 7), 2008. In 2009, tagging on the Northwest branch took place on May 8 (n = 25) and tagging on the Southwest branch took place on May 6 (n = 11) and May 7 (n = 14).

After recuperating from the initial stresses of angling, kelts were then anaesthetized in a mixture of water and clove oil (concentration of 40 mg/L). Once sufficiently anaesthetized (loss of equilibrium; absence of reactions to external stimuli) they were weighed (kg), measured (fork length, cm), scale sampled (for age determination), sexed (noted as male, female or fish whose sex could not be identified (“unknown”)) using secondary sexual characteristics and placed ventral side up into a U-shaped surgery board lined with wet mattress foam. All equipment used for surgery was first disinfected with diluted Wescodyne. During surgery, all surgery gear was disinfected in a mixture of distilled water and Furacin prior to each operation while tags were disinfected in 90% alcohol, rinsed and dried. A 2.5 – 3 cm incision was then made with a curved scalpel blade along the abdomen, slightly adjacent to the midline and just anterior of the pelvic girdle. The tag was inserted lengthwise into the interperitoneal cavity. The incision was then sutured closed with two to three interrupted sutures using a number two suture thread and curved needle. During the entire surgical procedure, the gills of the fish were continuously irrigated with fresh river water. In rare instances when fish showed any sign of reviving during surgery, we replaced the water used to irrigate the gills with a clove oil solution in order to deepen the anaesthesia. After surgery was completed (total time from removal from the anaesthetic bath to return to the recovery crates was about 2 to 5 min) kelts were placed in large wooden flow through recovery crates in the river. Kelt recuperation time from effects of anaesthetic was approximately five minutes. After a minimum of two hours for recovery, the kelt was released back into the river at the surgery site. This was done to ensure that no immediate mortality occurred from the surgery or from delayed reactions to the stresses of angling.

Data retrieval

Bay and coastal New Brunswick receivers were retrieved and downloaded periodically during each year. Units in the Strait of Belle Isle were initially downloaded mid July of 2008 and 2009, and again when these units were removed in late autumn. We were sent the data for kelts detected on arrays in Gilbert Bay in 2008 and Trinity Bay in 2009. The information stored in a download consisted of the fish ID, time and date of detection as well as the temperature and depth the fish was at.

Analyses

Statistical analyses were conducted using parametric and non-parametric tests as appropriate, following Zar (1999). Fish in the study were grouped in different ways depending on the analysis. These groupings are identified as results are reported.

Travel times and the amount of time a kelt spent within a particular area was calculated by taking the time of their first detection on a given receiver to the last detection of a given receiver. Kelts that frequented a given area or set of receivers more than once had each individual measure of time added together to give a total amount of time. All distances were measured as straight line distances. Speeds of travel were obtained using the calculated travel times over the measured straight line distances.

RESULTS

In 2008, tagged kelts (all ages and sexes combined) averaged 67.1 cm fork length (n = 50; range 53.4 – 89.3 cm) and had mean weights of 2.1 kg (n = 39; range 0.8 – 4.35 kg). Condition factors (K) averaged 0.61 (n = 39; range 0.45 to 0.77). A total of 30 1SW and 20 2SW kelts were tagged (21 males, 25 females, four unknown); 48 of the 50 kelts (96 %) exited the estuary. In 2009, kelts had an average length of 62.6 cm (n = 50; range 55.4 – 92.5 cm) and weight of 1.6 kg (n = 49; range 0.9 – 5.7 kg). Average K was 0.63 (n = 49; range 0.53 – 0.75). A total of 44 1SW and four 2SW and two 3SW kelts were tagged (33 males, 15 females, two unknown; see Appendix 1a, b for details); 46 of the 50 kelts (92 %) exited the estuary.

Migration

There are three main locations a kelt may travel once out of the Miramichi system: through the Strait of Belle Isle, through Cabot Strait or remain within the Gulf of St. Lawrence. Three kelts in 2008 were documented in the outer bay of the Miramichi system, traveling along the northern shore near Tabusintac shortly after exiting the inner bay. No kelts were detected along the southern shore at Escuminac Point. In 2009, no kelts were detected in the outer bay area.

Once kelts left the Miramichi system over the next year, they were detected at various locations within the Gulf and the Atlantic Ocean coast line (Figure 1).

In 2008, a total of 22 (45.8 %) kelts that exited the Miramichi estuary (9 males, 11 females, 2 unknown sex; these include 12 grilse, 10 salmon) travelled through the Strait of Belle Isle. The proportion of salmon to grilse that exited the estuary was 19:29 compared to the proportion that crossed the Strait of Belle Isle at 10:12. Twenty-one kelts originated from the Northwest branch and one from the Southwest branch. On the

Strait of Belle Isle array, two kelts were detected on receivers less than six kilometers from the Newfoundland coast, three on receivers less than six kilometers from the Labrador coast and 15 on receivers more than six kilometers from either shoreline in the middle of the Strait of Belle Isle. Two more salmon were detected on receivers near both the coast of Labrador and the middle of the strait. Eleven of the kelts crossed the line of receivers during the day, ten passed at night and one during the day and night.

In 2009, 9 kelts (19.6 % of those that exited the estuary system) passed through the Strait of Belle Isle: four originated from the Northwest branch and five from the Southwest branch. Of these, six were male, three were female and all were grilse. One and four kelts were detected near the Labrador and Newfoundland coasts, respectively and three in the middle of the strait. One additional kelt was detected both on the Labrador coast and in the middle channel. Six kelts crossed during the day, two at night and one during the day and night.

The synchronicity of passage through the Strait of Belle Isle differed between years (Figure 2). Kelt passage spanned 20 days (July 2 – 21) in 2008 and 35 days (June 27 – July 31) in 2009. A peak passage of 14 kelts over five days (July 4 – 8) was observed in 2008. There was no peak passage documented in 2009 and different individuals were only recorded twice passing the line of receivers on two consecutive days. Kelt detections were rarely (2008) or never (2009) closer than two hours apart. The amount of time kelts spent in range of the receivers was short, and averaged 0.8 h (range 0 – 7.1 h; average of 13 hits/fish (range 1 – 9 hits/fish)) in 2008 and 1.72 h (range 0 – 13.5 h; average of 14 hits/fish (range 1 – 38 hits/fish)) in 2009.

Three kelts that passed through the Strait of Belle Isle were subsequently detected on a limited coastal array at Gilbert Bay, Labrador about 175 km north of the Strait of Belle Isle. These kelts were detected at Ship Harbour, Fish Rock and Spear Point at the mouth of the bay area between July 7 and 24, 2008. Kelts spent less than 30 minutes in range of the receivers at these locations.

Of the consecutive spawners that returned to the Miramichi River system in 2008 (n =3) and 2009 (n = 4), two (one each year) were detected outside the barrier islands of the Tracadie River system, spending less than 20 minutes in the area. A lone kelt returned to the coastal area of Kouchibouguac on July 24, 2008 after crossing the line of receivers in the Strait of Belle Isle the first time on July 2 and again on July 13, 2008.

One alternate spawner tagged in 2008 and returning in 2009 was not detected exiting the Gulf via the Strait of Belle Isle exit in 2008. It was later detected in Trinity Bay, Newfoundland on May 22, 26 and 29, 2009 for a seven and a half day period. This kelt was then picked up on the New Brunswick coast of the Chaleur Bay on June 22, 2009 before returning to the Miramichi estuary on July 6, 2009 (Figure 1).

Travel time and speed

The average travel time and speed for kelts (all ages and sexes combined) exiting the Miramichi estuary (May 17 to June 7, 2008 and May 12 to 17, 2009 respectively) to the Strait of Belle Isle in 2008 was significantly faster (t-test, n = 31, $p < 0.05$) than in 2009 (44.6 d at 17.6 km/d versus 54.1 d at 14.7 km/d, respectively). No significant difference in speeds of travel was noted among males (all ages) between years (t-test, n = 15, $p > 0.05$). However, a significant difference was seen among females (all ages) between years (t-test, n = 14, $p < 0.05$; Table I).

In 2008, males and females and grilse and salmon took similar times to reach the Strait of Belle Isle (t-test, n = 20 and 22 respectively, $p > 0.05$). In 2009, males and females reached the Strait of Belle Isle at similar average travel times and speeds (t-test, n = 9, $p > 0.05$). No differences in travel times and speeds were seen between Northwest and Southwest branch originating kelts. There was a significant correlation between travel speed and condition factor (all kelts of all ages and sexes) in 2008 (Pearson correlation, r = 0.554, n = 17, $p < 0.05$), but not in 2009 (Pearson correlation, r = 0.135, n = 8, $p > 0.05$).

Kelts that passed through the Strait of Belle Isle were not significantly different at the time of tagging from kelts that were not detected passing through this exit in length (Mann-U, n = 48, $p > 0.05$), weight (Mann-U, n = 39, $p > 0.05$) or condition factor (t-test, n = 39, $p > 0.05$) in 2008 and in 2009 (length (Mann-U, n = 46, $p > 0.05$), weight (Mann-U, n = 45, $p > 0.05$) or condition factor (t-test, n = 45, $p > 0.05$)). There were also no differences found in the time and speed of travel within the Miramichi estuary between kelts that passed and did not pass through the strait in 2008 (t-test, n = 48, p > 0.05) and 2009 (Mann Whitney-U, n = 46, p > 0.05).

Three kelts reached the Gilbert Bay area in 2008, covering the distance of 175 km from the Strait of Belle Isle in an average time of 3.2 d (2.8 – 3.4 d) at speeds of 55.8 km/d (53.4 – 59 km/d). One kelt, returning to the coast of New Brunswick (Kouchibouguac) after crossing the Strait of Belle Isle, covered the 791 km distance in 11.3 d at a speed of 69.9 km/d in 2008. Another kelt tagged in 2008 was detected in 2009 (366 days later) in Trinity Bay before returning to the Miramichi system. As Trinity Bay is closer to Cabot Strait, it is assumed that the kelt took this entrance to reach Chaleur Bay on June 22, 2009 (1214.3 km) in 26.3 d at a speed of 46.2 km/d. From Chaleur Bay it took 15.7 d at a speed of 11.3 km/d to reach the barrier islands 176.6 km away.

The three consecutive spawners in 2008 spent an average of 50.2 d (44 – 57.4 d) out of the estuary system. Return dates were between July 11 and 18, 2008. Two of these three salmon returned again on July 6 and 12, 2009 after exiting the river in spring 2009 and spending an average of 57.4 d (50 – 64.8 d) at sea. Four consecutive spawners returned between June 30 and July 16, 2009 after an average of 46 d (44.4 – 48.4 d) out of the system.

The three alternate spawners tagged in 2008 that were detected in the Strait of Belle Isle returned to the river system in an average of 394.7 d after exiting the estuary in spring 2008 (366 – 413 d). Dates of return were between May 31 and July 12, 2009.

Depth and temperature of travel

Four kelts with T/P tags passed through the Strait of Belle Isle in 2008. Minimum and maximum depths of travel for all kelts ranged from 3.6 to 52.8 m. The depths available to kelts when crossing the Strait of Belle Isle array (measured from the depths at the receiver locations) ranged from 6.6 to 108.8 m. The average temperature these kelts experienced was 7.1 °C (2.7 – 8.65 °C). The lone kelt with a T/P tag that crossed the line in 2009 did so at an average depth and temperature of 5.4 m (4.9 – 6 m) and 7.9 °C (7.7 – 7.9 °C).

DISCUSSION

Migration

Upon exiting the Miramichi estuary, kelts entered the Gulf of St. Lawrence. They rarely were detected travelling along the New Brunswick coast, where receivers were in place from Miscou Island point to the north and Kouchibouguac to the south. This indicates that coastal waters may not play an important role in the migratory movements of kelts and that open waters are initially sought once in the Gulf of St. Lawrence. This may be due to higher salt concentration or greater currents, but we do not know what other environmental cues the kelts use to orient early migration.

Kelts originating from river systems inside the Gulf of St. Lawrence and proceeding to ocean feeding pastures off Greenland have two options for entering the Atlantic Ocean: the Strait of Belle Isle and Cabot Strait. We documented the passage of 22 and nine kelts using the Strait of Belle Isle in 2008 and 2009, respectively. These are probably minimum values as some kelts may have crossed the array undetected. Clearly, this Strait is an important migration pathway. The difference in the number of kelts that passed through the Strait of Belle Isle between the two years may be due to different portions of the population being tagged in each year. More females and salmon were tagged in 2008 than in 2009. These may utilize the Strait of Belle Isle exit in greater proportion than males and grilse. The use of the Strait of Belle Isle by smolt and bright salmon has been inferred in the past from fishery catches (Belding & Préfontaine, 1961; Caron, 1983). Recent telemetry studies have detected both smolt and kelts utilizing this passage to exit the Gulf (ICES, 2008a; Hedger *et al*., 2009). Hedger *et al*. (2009) reported a minimum passage of 13 kelts passing the line in 2007, but none in 2006.

The kelts that were not detected in the Strait of Belle Isle and which did not return to the Miramichi River system as consecutive spawners, may have passed through Cabot Strait or remained in the Gulf after exiting the estuary. Past research has suggested that Cabot Strait is also an important migratory route (Lagueux, 1953; Reddin, 1985). However, at the time of this work Cabot Strait was not equipped with sonic telemetry receivers.

Passage through the Strait of Belle Isle was primarily during the day. Kelts tended to swim offshore but closer to Labrador in 2008, but offshore and closer to the Newfoundland coast in 2009. Currents exiting the Gulf through the Strait of Belle Isle do so along the Newfoundland coast, whereas those that enter the Gulf do so along the Labrador shore (Templeman, 1967). It is possible that kelts swim with the main currents and tides to exit the strait, but it is likely that they travel against them as well, as documented by Hedger *et al*. (2009) in the Gaspé Bay.

Kelts passed through the Strait of Belle Isle between July 2 – 21 in 2008 and June 27 – July 31 in 2009. These kelts exited the Miramichi system between May 15 – June 3, 2008 and May 11 – 26, 2009, reaching the strait within a short time frame (average 44.6 d in 2008, 54 d in 2009). A similar time frame was seen in kelts studied by Hedger *et al*. (2009) leaving the Gaspé Bay, traveling 119 km less than kelts from the Miramichi and crossing the strait between July 1 – 15, 2007. Assuming that kelts from the Miramichi and York River exit the Gulf during the month of July every year, it is likely that the kelts from both river systems are in the area at the same time and may travel through a portion of the Gulf together, congregating before entering the Atlantic Ocean. More research is needed to determine if kelts from different rivers use the Strait of Belle Isle at the same time.

Even though most kelts crossed the line of receivers in 2008 within a five day period, typically tagged individuals were separated in their passage by > 2 hr. Only once did kelts cross just over 30 minutes apart. No peak was observed in 2009. Kelts from the Miramichi River may be traveling together for short periods in loose shoals. This could result in a continuous passage of individuals with small subgroups. The schooling pattern of kelts crossing the Strait of Belle Isle line of receivers may become clearer when taking into account kelts from different river systems that may mix with those from the Miramichi before leaving the Gulf.

Once at the Strait of Belle Isle, kelts spent little time within range of the VR2s (average of 0.8 h and 1.72 h in 2008 and 2009, respectively), traveling quickly through the strait to the Atlantic Ocean. The three kelts that reached Gilbert Bay crossed the Strait of Belle Isle array between the middle of the line and the Labrador coast. These may have cut toward the Labrador coast before exiting the strait to travel near shore to reach the Gilbert Bay area. Once again, little time was spent in the Gilbert Bay area (< 30 mins) suggesting that kelts that do travel along the coast line are stopping at given locations along the way before leaving the coast. The reason for traveling along the shore line and not heading directly to the open ocean is not known but kelts may take advantage of better feeding opportunities or temperature regimes.

Travel time and speed

The significant difference seen in the time and speed of travel between kelts that crossed the Strait of Belle Isle in 2008 and 2009 is possibly due to different exit dates in both years (May 17 to June 7, 2008 and May 12 to 17, 2009) from the Miramichi estuary system. In order to cross the Strait of Belle Isle array at approximately the same time period in both years, kelts that exited the estuary later would need to travel faster than those that exited earlier. It may also be attributed to the different proportion of males, females and grilse and salmon that were detected crossing the line of receivers. There were more females and salmon in 2008 and they also moved faster than the males and grilse of that year. There was also no difference in male travel speeds but a difference of female travel speeds between the years suggesting that the presence of females (most being salmon) is influencing this difference. The significant correlation seen between travel speed and condition factor in 2008 and not in 2009 may also be due to the salmon present in 2008. All the salmon in 2008 were female. These generally have greater energy reserves and thus possibly higher condition factors compared to males come spring (Jonsson *et al*., 1991b). This trend was seen in both years of this study. This may permit them to move through the Gulf more quickly than kelts that had less energy and a greater need to feed once out of the estuary.

There do not appear to be any biological characteristics (sex, age, size) or migratory characteristics (travel time and speed within the estuary) evident in this study that could aid in distinguishing if a kelt should pass through the Strait of Belle Isle. This suggests that the governing factor may be genetic (river of origin), environmental (prey abundance, temperature or currents) or social.

The speeds of travel attained by kelts in this study have exceeded the reported maximum sustainable swimming velocity for kelts (0.5 m/s for 200 minutes or 43.2 km/d;

Hubley *et al*., 2008). Speeds of travel increased throughout the kelt's migration from the estuary system (average 6.5 km/d in 2008, average 9.3 km/d in 2009) through the Gulf (average 17.6 km/d in 2008 and 14.7 km/d in 2009) and to Gilbert Bay (average 55.8 km/d) in 2008. Similar speeds of 15 km/d through the Gulf were documented by Hedger *et al*. (2009), taking kelts an average time of 45 d to reach the line of VR2s, fewer days than reported in this study. The small increase in speed between the estuary and Gulf may be due to the time needed for acclimation and initial feeding in the estuary that is not required in the Gulf. The marked increase in speed from the Strait of Belle Isle to Gilbert Bay may be due to a need to feed and hence rapidly reach their feeding ground in the Labrador Sea, but a greater understanding of what kelts are doing in the Gulf and Atlantic Ocean is needed to explain these differences.

The opposite pattern was seen in speed of travel for kelts returning to the river system as a repeat spawner. These fish crossed the Gulf at a speed of 46.2 km/d to Chaleur Bay then continued to the Miramichi estuary at a speed of 11.3 km/d. This decrease in speed may be due to increased exploration by the salmon to locate its natal river which may involve entering different bays and estuaries along their trajectory until the destination is reached.

Consecutive and alternate spawners

Consecutive spawners in this study spent, on average, less than two months outside the Miramichi system before returning to spawn. This is less than the two to five months documented via the trapnets located near the head of tide in the Miramichi estuary (O'Connell *et al*., 2006; Chaput *et al*., 2010). Only one of the kelts, a two-time repeat spawner, spent more than two months outside the system. This earlier return time is expected as telemetry studies give a truer measure of arrival and residence times than other methods being used to sample fish that may only provide data on their arrival at a considerable time after they have arrived. Estuary return dates fell between the end of June and middle of July. Return times were similar to those reported for kelts in Newfoundland rivers (average 66.1 d; Reddin *et al*., 2004), but less than reported for the lone kelt from the LaHave River, Nova Scotia (79 d; Hubley *et al*., 2008).

The general consensus among researchers is that consecutive spawners remain relatively close to their river of origin during their short return to the sea (Reddin *et al*., 2004; Niemelä *et al*., 2006). We documented a maximum speed of travel of 69.9 km/d for a kelt crossing the Gulf of St. Lawrence returning to the coastal waters of New Brunswick on July 24 after reaching the Strait of Belle Isle on July 2 and again July 13, 2008. It is possible that this kelt had reconditioned (at least in part) in order to spawn consecutively. Although we did not document this fish entering the Miramichi River to spawn it may have ascended another river system or died before reaching its final destination. The trajectory of this fish shows that there is a possibility for adult salmon (including consecutive spawners) to travel farther from their natal rivers than previously believed.

Using the average amount of time consecutive spawners spent out of the river system, the maximum speed recorded (69.9 km/d) and the average speed kelts traveled to reach the Strait of Belle Isle (16.2 km/d) in this study, we calculated the total straight-line distance kelts can travel and still return within the same time frame as consecutive spawners to be between 829.44 to 3578.88 km return, or 414.72 to 1789.44 km one way. These distances can take kelts as far as the Quebec north shore and Cabot Strait within the Gulf to well into the Labrador Sea and Grand Banks of Newfoundland. In order for kelts to recondition one must assume that long periods are spent feeding and not traveling, reducing these calculated maximum distances. The recent increase in consecutive spawners returning to the Miramichi River has been associated with an increase in baitfish abundance in the Gulf region (ICES, 2008b). It is possible that kelts from the Miramichi River travel throughout the Gulf of St. Lawrence feeding on the higher densities of baitfish that may occur in the different areas. Further research is needed on the movements of consecutive spawners to determine their migratory pathways and see what may regulate the time it takes to recondition.

Of the four alternate spawners, three were not detected in the period between leaving the Gulf area through the Strait of Belle Isle and returning to the river a year later. The fourth was not detected exiting the Gulf, but was later detected returning along the coast of Newfoundland and New Brunswick before entering the river system. It is assumed that these kelts were fully reconditioned and able to spawn. The entrance to the Gulf during their return that these reconditioned kelts took is unknown, but they most likely passed into this area in late May to early June as no kelts were detected in the Strait of Belle Isle after the receivers were deployed in mid-June. Kelts may also have entered via Cabot Strait as one kelt was detected in southeast Newfoundland (Trinity Bay) before detection in the Gulf. Both entrances to the Gulf are most likely used for returning repeat spawners (Lagueux, 1953; Belding & Préfontaine, 1961; Templeman, 1967, 1968; Reddin, 1985).

Once in the Atlantic Ocean, North American alternate spawners have been documented feeding and overwintering in the North Atlantic Ocean from the Davis Strait and Labrador Sea south to the Grand Banks of Newfoundland (Lagueux, 1953; Templeman, 1967, 1968; Lear, 1972; Reddin, 1985; Friedland *et al*., 1993). Occasional detections of Miramichi salmon north of the Faroe Islands have also occurred (Hansen & Jacobsen, 2003). It has been suggested that Atlantic salmon distribution in the North Atlantic Ocean is regulated by sea surface temperature (Friedland *et al*., 1993; Martin & Mitchell, 1985; Friedland *et al*., 1998). It is therefore possible that the four alternate spawners in this study remained either in the north or south of the North Atlantic Ocean in waters around the Labrador Sea and Grand Banks or that they travelled between these areas during the year before returning. There are also indications that alternate spawners and maiden salmon from North America and Europe may frequent separate areas of the ocean (Niemelä *et al*., 2006), but further research is needed to see if this may be the case for salmon from the Miramichi River system.

Depth and temperature of travel

Average temperatures experienced by kelts crossing the Strait of Belle Isle were similar (between 7 and 8 °C) in 2008 and 2009. This is near the temperature range of 8 – 10 °C believed to be optimal for postsmolts in the North Sea area (Friedland *et al*., 1998). Whether temperature affects kelts in the same manner as postsmolts is not known.

Their depth of travel was variable, never less than three meters in both years. This differs from Hedger *et al*. (2009) who reported 78 % of depth detections to be less than one meter. The depths recorded in this study were also deeper than the maximum of 4 m recorded by Templeman (1967, 1968) in the Atlantic Ocean. This indicates that kelts may routinely take advantage of a wide range of depths either for foraging, locating temperature boundaries or other unknown factors.

CONCLUSION

This study documented the use of the Strait of Belle Isle as an important migratory pathway over a short period of time for kelts reaching the Atlantic Ocean. During their migration through the Gulf of St. Lawrence, there are indications that kelts from the Miramichi and other river systems may be congregating before passing through the Strait. Further research is needed to determine whether they are waiting for adequate numbers, or the right environmental conditions before continuing their migration. Increases in speed as kelt migration progressed suggests that feeding and time to acclimate decreases as the kelt approach their grounds within the Atlantic Ocean.

Consecutive spawners returned after short stints away from the Miramichi system. Documented speeds of travel within the Gulf indicate that this spawning group may travel far within the Gulf, or may even exit it to recondition. This is different for alternate spawners that enter the Atlantic Ocean, occasionally traveling along the coast as they leave and return to the river system.

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Table I: a) The average time (days, range) and speed traveled (km/day, range) to the Strait of Belle Isle from the outer array for all kelts, males (all ages), females (all ages), grilse (all sexes) and salmon (all sexes) in 2008. b) The average time (range) and speed traveled (range) to the Strait of Belle Isle from the outer array for all kelts, males (all ages) and females (all ages) in 2009.

a)

2008	All Kelts*	Males	Females*	Grilse	Salmon
Time	46.6 (34.5 – 63.5)	45 (34.5 – 53.5)	42.9 (34.5 – 54.4)	46.2 (34.5 – 3.5)	42.7 (34.5 – 54.4)
Speed	17.6 (12.1 – 22.3)	17.3 (14.4 – 22.2)	18.2 (14.1 – 22.3)	17 (12.1 – 22.2)	18.3 (14.1 – 22.3)

b)

2009	All Kelts*	Males	Females*
Time	54.1 (42.4 – 74)	54.4 (42.4 – 74)	53.6 (42.4 – 61.2)
Speed	14.7 (10.4 – 18.2)	14.7 (10.4 – 18.2)	14.7 (12.6 – 18.1)

* Denotes a significant difference between the two years (2008 and 2009) for the specified groups (all kelts – time and speed, females – speed)

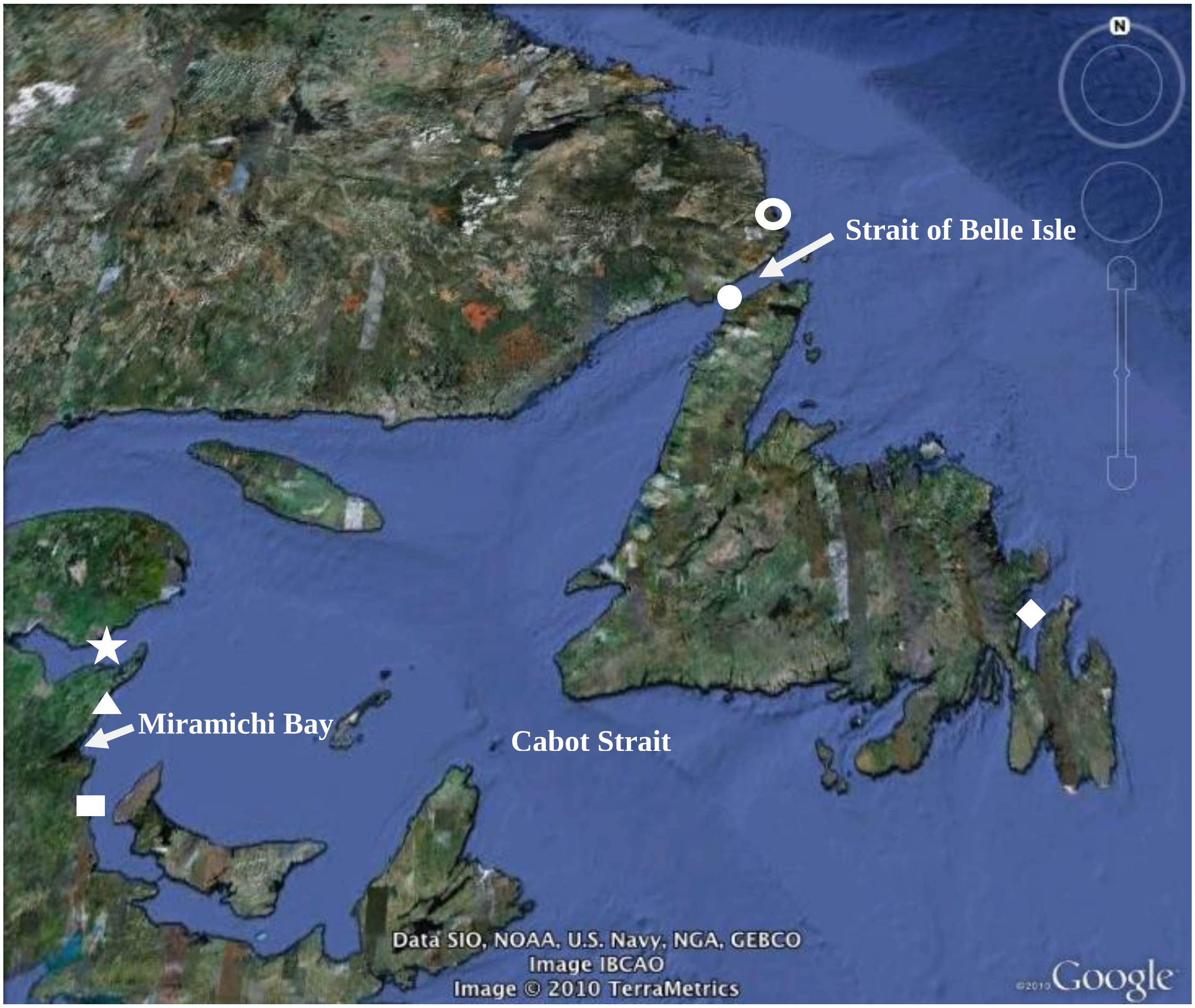

Figure 1: Map of the Gulf of St. Lawrence and Atlantic coast line showing the Strait of Belle Isle, Cabot Strait, the Miramichi Bay and detection locations of different kelts (Star – Chaleur Bay, Triangle – Tabusintac, Rectangle – Kouchibouguac, Open circle – Gilbert Bay, Circle – Strait of Belle Isle, Diamond – Trinity Bay).

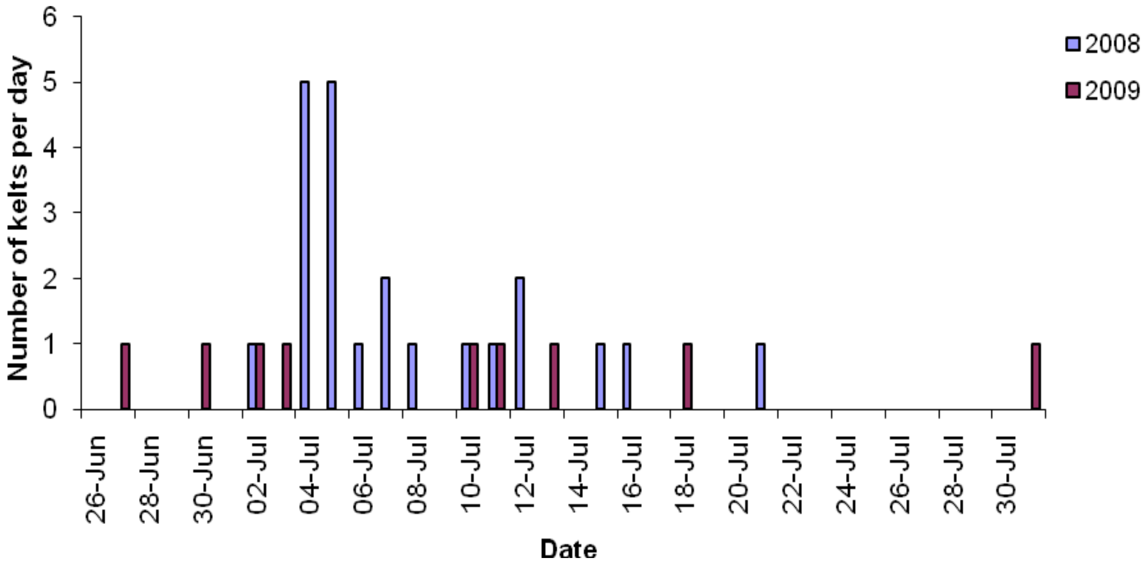

Figure 2: The number of kelts that crossed through the Strait of Belle Isle per day in 2008 and 2009.

CONCLUDING STATEMENT

Low mortality rates within the Miramichi estuary suggest that major kelt mortality is occurring in the Gulf or Atlantic Ocean. Catch-and-release angling does not appear to cause significant mortality for kelts, and released fish subsequently undertake extensive migrations. Kelts spent a large amount of time in the area of their release location at the head-of-tide of the estuary. The time spent here may help their long-term survival as they feed on smelt and recuperate after tagging. Further research is needed to determine the amount of time kelts take to recuperate from surgery before resuming normal behavior and if kelts remaining in this area are indeed feeding or just recovering. The importance that early feeding plays in kelt survival should also be determined.

Outside of the Miramichi system, kelts used the Strait of Belle Isle to exit the Gulf in both years. This occurred over a short period of synchronous passage. The use if any of the Cabot Strait is currently unknown. Further research taking advantage of the expanding network of receivers placed as part of the Ocean Tracking Network will enable researchers to document this passage. Similarly, expanding kelt tagging to different river systems within the Gulf will provide insight into how different populations may interact or congregate before leaving the Gulf.

The distances consecutive spawners travel may be farther than previously believed (about 100 km away), possibly exiting the Gulf, while alternate spawners were documented throughout the coastal areas of the Atlantic Ocean. Continued research using acoustic telemetry to document repeat spawner migration can also benefit from the expanding Ocean Tracking Network to identify the migratory routes and destinations of Atlantic salmon kelts.

APPENDICES

Appendix 1a: The ID, date, release location, tag type and biological characteristics of kelts tagged in 2008 in the Miramichi estuary.

ID	Date	Release location	Tag type	Sex	Sea winter age	Weight (kg)	Length (cm)	Condition factor
49365	May 7 2008	Northwest branch	Coded	Male	1	-	59.5	-
49366	May 7 2008	Northwest branch	Coded	Male	1	-	65.2	-
49367	May 7 2008	Northwest branch	Coded	Male	1	-	57	-
49368	May 7 2008	Northwest branch	Coded	Male	1	-	60.8	-
49369	May 7 2008	Northwest branch	Coded	Female	1	-	56	-
49370	May 8 2008	Southwest branch	Coded	Male	1	1.5	65.2	0.5411883
49371	May 14 2008	Northwest branch	Coded	Female	2	4.35	82.7	0.7690821
49372	May 14 2008	Northwest branch	Coded	Female	2	3.5	78.2	0.7318933
49373	May 14 2008	Northwest branch	Coded	Female	2	2.7	78.4	0.5602934
49374	May 14 2008	Northwest branch	Coded	Male	1	1.3	60.4	0.5899735
13539	May 7 2008	Northwest branch	T/P	Male	1	-	65	-
13540	May 7 2008	Northwest branch	T/P	Female	1	-	55.3	-
13541	May 7 2008	Northwest branch	T/P	Male	1	-	58	-
13542	May 7 2008	Northwest branch	T/P	Unknown	1	-	61.5	-
13543	May 7 2008	Northwest branch	T/P	Female	2	-	79.5	-

13544	May 7 2008	Northwest branch	T/P	Female	2	-	79.8	-
13545	May 9 2008	Northwest branch	T/P	Female	2	2.65	74.6	0.6383066
13546	May 9 2008	Northwest branch	T/P	Female	1	0.9	54.6	0.5529229
13547	May 9 2008	Northwest branch	T/P	Unknown	1	0.8	53.4	0.5253711
13548	May 9 2008	Northwest branch	T/P	Male	1	1.35	58.2	0.6848016
13549	May 8 2008	Southwest branch	T/P	Female	2	2.3	75.4	0.5365544
13550	May 13 2008	Southwest branch	T/P	Female	2	3.45	79.4	0.6892195
13551	May 13 2008	Southwest branch	T/P	Male	1	1.4	61.2	0.6107644
13552	May 13 2008	Southwest branch	T/P	Male	1	1.45	59.4	0.6918447
13553	May 13 2008	Southwest branch	T/P	Female	2	3.6	83.5	0.6183624
13554	May 13 2008	Southwest branch	T/P	Female	2	3.4	80.1	0.6615784
13555	May 13 2008	Southwest branch	T/P	Female	2	3.65	80	0.7128906
13556	May 13 2008	Southwest branch	T/P	Male	1	1.25	58.8	0.6148625
13557	May 14 2008	Northwest branch	T/P	Male	1	1.1	56.5	0.6098841
13558	May 14 2008	Northwest branch	T/P	Male	1	1.1	56.8	0.6002714
49400	May 9 2008	Northwest branch	Coded	Female	2	2.7	79.3	0.5414323
49444	May 9 2008	Northwest branch	Coded	Female	2	2.85	77.6	0.6099014
49445	May 9 2008	Northwest branch	Coded	Female	2	3.3	79.4	0.6592534

49446	May 9 2008	Northwest branch	Coded	Unknown	1	0.8	56.2	0.4506932
49447	May 9 2008	Northwest branch	Coded	Female	2	3.2	78.2	0.6691596
49448	May 9 2008	Northwest branch	Coded	Female	2	3.6	80.4	0.6926827
49449	May 9 2008	Northwest branch	Coded	Female	2	2.2	74.6	0.5299149
49450	May 9 2008	Northwest branch	Coded	Male	1	1.9	67.5	0.617792
49451	May 9 2008	Northwest branch	Coded	Male	1	1.35	62.4	0.5556227
49452	May 9 2008	Northwest branch	Coded	Male	1	1.25	58.8	0.6148625
49453	May 14 2008	Northwest branch	Coded	Unknown	1	1.15	57.4	0.608082
49454	May 14 2008	Northwest branch	Coded	Female	2	3.85	89.3	0.5406377
49455	May 14 2008	Northwest branch	Coded	Male	1	1.05	59.5	0.4984692
49456	May 14 2008	Northwest branch	Coded	Female	2	2.9	76.8	0.640198
49457	May 14 2008	Northwest branch	Coded	Female	1	0.95	53.5	0.6203863
49458	May 14 2008	Northwest branch	Coded	Male	1	1.15	59.6	0.5431991
49459	May 14 2008	Northwest branch	Coded	Male	1	1.05	55.8	0.6043474
49460	May 14 2008	Northwest branch	Coded	Female	2	2.15	71.5	0.5881936
49461	May 14 2008	Northwest branch	Coded	Male	1	1.4	65	0.509786
49462	May 14 2008	Northwest branch	Coded	Female	1	1.25	57.8	0.6473311

Appendix 1b: The ID, date, release location, tag type and biological characteristics of kelts tagged in 2009 in the Miramichi estuary.

ID	Date	Release location	Tag type	Sex	Sea winter age	Weight (kg)	Length (cm)	Condition factor
57877	May 8 2009	Northwest branch	Coded	Female	1	0.9	55.4	0.000588126
57878	May 8 2009	Northwest branch	Coded	Male	1	1.05	56.7	0.000548594
57879	May 8 2009	Northwest branch	Coded	Unknown	1	1.3	59.2	0.000481987
57880	May 8 2009	Northwest branch	Coded	Male	1	1.35	61.8	0.000423677
57881	May 8 2009	Northwest branch	Coded	Female	1	1.3	59	0.000486905
57882	May 8 2009	Northwest branch	Coded	Female	1	1.1	55.7	0.000578675
57883	May 8 2009	Northwest branch	Coded	Male	1	1.3	58	0.000512526
57884	May 8 2009	Northwest branch	Coded	Female	1	1.2	57.2	0.000534333
57885	May 8 2009	Northwest branch	Coded	Male	1	1.15	57.5	0.000526013
57886	May 8 2009	Northwest branch	Coded	Female	1	1.35	60	0.000462963
57887	May 8 2009	Northwest branch	Coded	Male	1	1.55	62.8	0.000403758
57888	May 8 2009	Northwest branch	Coded	Male	1	1.6	64	0.00038147
57889	May 8 2009	Northwest branch	Coded	Male	1	1.3	60.1	0.000460656
57890	May 8 2009	Northwest branch	Coded	Unknown	1	1	55.7	0.000578675
57891	May 8 2009	Northwest branch	Coded	Male	1	1.25	58.2	0.000507261
57892	May 8 2009	Northwest branch	Coded	Male	1	1.7	63.1	0.000398026

57893	May 8 2009	Northwest branch	Coded	Male	1	1.5	61.3	0.000434129
57894	May 8 2009	Northwest branch	Coded	Male	1	1.5	60.9	0.000442739
57895	May 8 2009	Northwest branch	Coded	Male	1	1.6	65.5	0.000355857
57896	May 8 2009	Northwest branch	Coded	Male	1	1.5	63.2	0.00039614
57897	May 8 2009	Northwest branch	Coded	Female	2	3.4	81.1	0.000374945
57898	May 8 2009	Northwest branch	Coded	Male	1	1.8	66	0.000347831
57899	May 6 2009	Southwest branch	Coded	Male	1	1.65	66	0.000347831
57900	May 6 2009	Southwest branch	Coded	Male	1	1.35	59	0.000486905
57901	May 6 2009	Southwest branch	Coded	Male	1	1.2	58.5	0.000499496
57902	May 6 2009	Southwest branch	Coded	Male	1	1.35	59	0.000486905
57903	May 6 2009	Southwest branch	Coded	Male	1	1.3	59	0.000486905
57904	May 6 2009	Southwest branch	Coded	Female	1	1.1	55.7	0.000578675
57905	May 6 2009	Southwest branch	Coded	Male	1	1.25	59.5	0.000474733
57906	May 6 2009	Southwest branch	Coded	Male	1	1.35	58.7	0.000494408
57907	May 6 2009	Southwest branch	Coded	Male	1	1.4	59.5	0.000474733
57908	May 7 2009	Southwest branch	Coded	Male	1	1.3	59.6	0.000472347
57909	May 7 2009	Southwest branch	Coded	Male	1	1.6	63	0.000399925
57910	May 7 2009	Southwest branch	Coded	Male	1	1.45	62	0.00041959

57911	May 7 2009	Southwest branch	Coded	Male	1	1.4	63.6	0.000388713
57912	May 7 2009	Southwest branch	Coded	Female	3	4.6	85	0.0004885
57913	May 7 2009	Southwest branch	Coded	Female	1	1.3	60.5	0.000451579
57914	May 7 2009	Southwest branch	Coded	Female	3	5.7	92.5	0.00037905
57915	May 7 2009	Southwest branch	Coded	Male	1	1.55	61.5	0.000429907
57916	May 7 2009	Southwest branch	Coded	Male	1	1.1	57	0.000539977
57917	May 7 2009	Southwest branch	Coded	Female	1	1.1	58	0.000512526
57918	May 7 2009	Southwest branch	Coded	Female	1	1.3	59	0.000486905
57919	May 7 2009	Southwest branch	Coded	Male	1	1.6	61.5	0.000429907
57920	May 7 2009	Southwest branch	Coded	Female	2	2.95	77.5	0.00042966
57921	May 7 2009	Southwest branch	Coded	Male	1	1.3	58.2	0.000507261
57957	May 8 2009	Northwest branch	T/P	Male	2	2.1	68.5	0.000622241
57958	May 8 2009	Northwest branch	T/P	Male	1	1.75	64.6	0.000370939
57959	May 8 2009	Northwest branch	T/P	Female	2	3.8	81.2	0.000373561
57960	May 6 2009	Southwest branch	T/P	Female	1	-	61	-
57961	May 6 2009	Southwest branch	T/P	Male	1	1.1	57	0.000539977

Appendix 2a: The chi squared goodness-of-fit analyses for kelts from their release point and the first receiver downstream tagged in 2008.

	From release			From first receiver downstream		
ID	Chi Square calculated value		Chi squared tabulated value	Chi Square calculated value		Chi squared tabulated value
49365	1127384.882	>	5.991	10216.64242	>	5.991
49366	1115324.268	>	5.991	5494.892268	>	5.991
49367	2177528.176	>	5.991	51073.12866	>	5.991
49368	1652322.791	>	5.991	438365.321	>	5.991
49369	871055.4783	>	5.991	51898.46778	>	5.991
49370	332101.6245	>	5.991	41200.66059	>	5.991
49371	862193.3264	>	5.991	672586.7241	>	5.991
49372	355276.9231	>	5.991	314160.5159	>	5.991
49373	242010.0319	>	5.991	273442.1385	>	5.991
49374	118336.7923	>	5.991	220812.7679	>	5.991
13539	1042544.114	>	5.991	30740.24963	>	5.991
13540	963054.2464	>	5.991	947436.5456	>	5.991
13541	774724.3492	>	5.991	865680.6601	>	5.991
13543	1443490.461	>	5.991	105958.4325	>	5.991
13544	674098.1506	>	5.991	47461.5274	>	5.991
13545	415024.2028	>	5.991	150877.8684	>	5.991
13546	829122.1022	>	5.991	309934.1903	>	5.991
13547	801911.9763	>	5.991	1393818.734	>	5.991
13548	952142.7388	>	5.991	9873.758338	>	5.991
13549	275451.1879	>	5.991	287672.7377	>	5.991
13550	491593.3539	>	5.991	128088.2696	>	5.991
13551	152362.3756	>	5.991	12042.25679	>	5.991
13552	2485480.561	>	5.991	62650.45775	>	5.991
13553	1096140.716	>	5.991	97010.39697	>	5.991
13554	2008397.758	>	5.991	105783.3142	>	5.991
13555	723042.2873	>	5.991	53148.82036	>	5.991
13556	1018968.209	>	5.991	233826.2329	>	5.991
13557	447283.0791	>	5.991	26323.41467	>	5.991
13558	173434.6835	>	5.991	12586.5542	>	5.991
49400	1126425.055	>	5.991	65043.62059	>	5.991
49444	1015623.921	>	5.991	136784.7097	>	5.991

49445	543766.1305	>	5.991	250252.5152	>	5.991
49446	944120.6138	>	5.991	18404.9901	>	5.991
49447	2148503.07	>	5.991	1048090.177	>	5.991
49448	801524.753	>	5.991	1016725.445	>	5.991
49449	1163668.632	>	5.991	67832.94227	>	5.991
49450	655946.0158	>	5.991	76548.68991	>	5.991
49451	1903872.573	>	5.991	699130.0882	>	5.991
49452	1093748.403	>	5.991	48491.51922	>	5.991
49453	438197.8121	>	5.991	202971.8688	>	5.991
49454	775500.9727	>	5.991	132262.1753	>	5.991
49455	253199.4215	>	5.991	33367.67823	>	5.991
49456	421665.8901	>	5.991	120391.6795	>	5.991
49457	1265844.503	>	5.991	314826.0807	>	5.991
49458	71848.03609	>	5.991	18362.96788	>	5.991
49459	322869.9055	>	5.991	56162.93199	>	5.991
49461	616391.2837	>	5.991	26649.73088	>	5.991
49462	458027.9542	>	5.991	40773.08478	>	5.991

Appendix 2b: The chi squared goodness-of-fit analyses for kelts from their release point and the first receiver downstream tagged in 2009.

	From release			From first receiver downstream		
ID	Chi Square calculated value		Chi squared tabulated value	Chi Square calculated value		Chi squared tabulated value
57957	557539.6483	>	5.991	441571.4727	>	5.991
57958	1215134.548	>	5.991	766173.1076	>	5.991
57959	1279966.251	>	5.991	1188435.964	>	5.991
57877	79029.18354	>	5.991	13929.55199	>	5.991
57878	1116287.035	>	5.991	1205.331441	>	5.991
57879	1534530.095	>	5.991	292919.985	>	5.991
57880	446575.7408	>	5.991	284429.0849	>	5.991
57881	54948.60607	>	5.991	11147.07253	>	5.991
57882	1613076.399	>	5.991	353053.863	>	5.991
57884	549078.1522	>	5.991	44004.79226	>	5.991
57886	351260.7918	>	5.991	1143.101868	>	5.991
57889	1540879.45	>	5.991	318740.7297	>	5.991

57890	115679.1182	>	5.991	42926.4467	>	5.991
57892	115679.9376	>	5.991	6351.810259	>	5.991
57893	466400.7775	>	5.991	854961.0281	>	5.991
57894	103382.5035	>	5.991	2174.370748	>	5.991
57895	146868.8178	>	5.991	4377.911512	>	5.991
57896	215582.1486	>	5.991	141836.0416	>	5.991
57897	2090078.46	>	5.991	139264.1098	>	5.991
57898	640704.6427	>	5.991	144275.1512	>	5.991
57960	861932.2115	>	5.991	6268.517611	>	5.991
57961	433182.2945	>	5.991	29524.93588	>	5.991
57899	148754.5339	>	5.991	11836.28194	>	5.991
57900	478263.461	>	5.991	53322.48162	>	5.991
57901	599517.3093	>	5.991	13281.24697	>	5.991
57902	478293.1267	>	5.991	101873.9651	>	5.991
57903	1240332.272	>	5.991	157658.5746	>	5.991
57904	478086.7687	>	5.991	26495.38495	>	5.991
57905	451106.4416	>	5.991	491352.3945	>	5.991
57906	217532.7743	>	5.991	66839.53349	>	5.991
57907	562641.3481	>	5.991	30544.43622	>	5.991
57908	600656.7329	>	5.991	56818.72225	>	5.991
57909	337857.8305	>	5.991	10918.947	>	5.991
57911	632985.8767	>	5.991	188218.8965	>	5.991
57912	717437.5319	>	5.991	87136.80275	>	5.991
57913	1381869.903	>	5.991	7004.937474	>	5.991
57915	1128144.328	>	5.991	10412.41864	>	5.991
57916	577339.6526	>	5.991	16331.15276	>	5.991
57917	691491.0742	>	5.991	302.107457	>	5.991
57918	380154.5221	>	5.991	26309.16928	>	5.991
57921	530130.8851	>	5.991	7739.92414	>	5.991

Appendix 3a: The chi squared goodness-of-fit analyses for repeat spawners tagged in 2008 returning back to the estuary and migrating upstream in 2008.

ID	Chi Square calculated value		Chi squared tabulated value
13550	463942.2915	>	5.991
13555	1623112.217	>	5.991
49372	122067.3516	>	5.991

Appendix 3b: The chi squared goodness-of-fit analyses for repeat spawners tagged in 2008 returning back to the estuary and migrating upstream in 2009.

ID	Chi Square calculated value		Chi squared tabulated value
13550	404609.3871	>	5.991
49371	57555.8039	>	5.991
49372	7775.471136	>	5.991
49448	23014.32081	>	5.991
49456	2000.892494	>	5.991

Appendix 3c: The chi squared goodness-of-fit analyses for repeat spawners tagged in 2009 returning back to the estuary and migrating upstream in 2009.

ID	Chi Square calculated value		Chi squared tabulated value
57959	2836.357551	>	5.991
57892	7812.346942	>	5.991
57898	25686.02569	>	5.991
57912	29736.62405	>	5.991