SEASONAL MIGRATIONS OF THE AMERICAN EEL, *ANGUILLA ROSTRATA*, IN THE UPPER SALMON RIVER, NEW BRUNSWICK

by

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ABSTRACT

Stable isotope analysis of American eels (*Anguilla rostrata*) captured in the Upper Salmon River, New Brunswick, revealed isotopic patterns suggesting that yellow-stage eels may be migrating between saline summer foraging grounds and freshwater overwintering habitat. We examined the seasonal movements of yellow eels in the Upper Salmon River using passive integrated transponder (PIT) and radio telemetry. Comparisons of isotopic signature and seasonal movements of 288 individual eels captured in fresh water in the spring of 2009 and 2010 showed that eels with enriched vs. depleted isotopic ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$), were more likely to migrate to the estuary in spring following release where they remained before exhibiting the reverse migration in fall; confirming that seasonal amphidromous migrations were driving the observed isotopic variation. Summer habitat residency in the estuary was confirmed in 2009 and 2010 using a manual PIT detection survey which showed that 36% and 34%, respectively, of spring-captured yellow eels PIT tagged and released in fresh water were identified resting in dense mats of sea lettuce (*Ulva intestinalis*). Freshwater overwintering of amphidromous eels was confirmed via radio tracking of select eels in the winter of 2009 and 2010. An examination of the environmental correlates of amphidromous eel migrations using count regression models determined that temperature and photoperiod were positive and negative correlates, respectively, of spring downstream migration. In addition, temperature and discharge were identified as negative and positive correlates, respectively, of fall upstream migration. Fall migration was also found to correlate significantly with the lunar cycle, with two peaks in migration

occurring prior to the new and full moons. Almost all migration occurred during periods of darkness, centered about 3.3 and 4.0 h post-sunset in the springs of 2009 and 2010, and 5.9 h post sunset in the fall of 2009. In all cases, migration was centered about the midpoint of the dark period. Spring eel migrations peaked 3.7 and 6.3 h following high tide in 2009 and 2010, respectively. However, fall upstream migration was randomly distributed with respect to tide. Mark and recapture models estimated that 10,220 (97.5% CI: 6139-16,540) and 3022 (97.5% CI: 2158-5073) yellow eels $\geq$20 cm in length migrated downstream in spring 2009 and 2010, respectively. Fyke nets and rotary screw traps (RST) sampled contrasting components or size classes of the migrating eel population. An RST retention test determined that eels <20.6 cm in length were likely to escape the RST holding box. In contrast, fyke nets did not appear efficient in capturing larger eels (i.e., >20 cm in length). RST modifications are warranted for future monitoring programs.

DEDICATION

This thesis is dedicated to my wife, Jenn, for leaving your prairie life behind and providing unending love, understanding, and support. I couldn't have done this without you and am forever indebted.

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1. GENERAL INTRODUCTION

1.1. BACKGROUND

The American eel, *Anguilla rostrata*, is a member of the "freshwater eel" family Anguillidae, and inhabits the western North Atlantic Ocean and coastal and inland waters of most of eastern North America. It is a panmictic species (Gagnaire et al. 2012) meaning the entire American eel population comprises one interbreeding group. As a panmictic species, the American eel exhibits remarkable phenotypic plasticity which enables members of the same species to survive in extremely diverse habitats ranging from tropical climates in the south to cold climates in the north (Jessop 2010). The American eel has a complex life cycle characterized by five life stages. Each year, mature eels leave the rivers and coastal areas throughout their distribution and migrate to a single location within the Atlantic Ocean for spawning; the western Sargasso Sea. However, the exact spawning location within the Sargasso Sea remains unknown and the general location of spawning has been determined based on the locations of the smallest larvae identified (Schmidt 1923; Schoth and Tesch 1982). Eels are believed to perish after spawning as no eels have returned to the coast subsequent to this migration. Therefore, the American eel is a semelparous species, meaning their reproductive strategy is characterized by a singular, and fatal, reproductive event. After hatching, young eels develop into leptocephali, which resemble a willow leaf. These larvae are passively transported and distributed by ocean currents from their spawning grounds in

the Sargasso Sea to coastal habitats within their continental range (Schmidt 1923; Kleckner and McCleave 1982). Due to the nature of this distribution process, it is believed that the spawning location is in an area that maximizes distribution by ocean currents (Tsukomoto et al. 2002). Upon nearing the coast, eels transform into the second life stage; the glass eel stage, in which active migration toward fresh water commences (Tesch 2003). Glass eels are so-named due to their transparent form. Typically, as their migration progresses, eels develop pigment and are then referred to as elvers; the third life stage. In contrast to leptocephali, glass eels and elvers are similar in form to the elongated adult and can pass high vertical barriers such as waterfalls by adhering to and climbing up wet vertical surfaces (Legault 1988; Knights and White 1998). This allows the American eel to inhabit inland waters that other diadromous species, such as Atlantic salmon (*Salmo salar*), can't reach. Upon reaching target habitat, American eels revert to an extended feeding and growth stage known as the yellow eel stage. This is the fourth and longest life stage of the American eel lasting from 5 to 40 years in Atlantic Canadian waters (Jessop 1987). Once a sufficient amount of growth has occurred, American eels then undergo a transformation into the fifth and final life stage; the silver eel phase. Silver eels are the mature form of the American eel and are specialized for long-term migration and spawning. Transformation from the yellow to silver eel stage includes a graying or silvering of the skin pigment, enlargement of the pectoral fins and eyes which are likely conditioning factors for the long-distance oceanic migration to the Sargasso Sea, and increased fat storage which, in addition to fueling the migration, is required for the development of eggs in females (Tesch 2003).

Anguillid eels have also long been used as a textbook example of a fish species exhibiting a catadromous life cycle (Myers, 1949), meaning that they are resident to freshwater environments during the feeding and growth period but migrate to saltwater environments to spawn. However, recent otolith microchemistry studies have suggested that many anguillid eels spend their entire lives in coastal salt waters before returning to the ocean to spawn and, therefore, are not obligate catadromous species as previously believed (Lamson et al. 2006; Thibault et al. 2007a; Jessop et al. 2008). This observation has lead researchers to suggest a more appropriate term for the nature of the eel's life cycle: facultative catadromy (Tsukomoto and Arai 2001; Thibault 2007a).

In 2003, as part of the annual meeting of the American Fisheries Society in Québec City, the International Eel Symposium culminated in the release of the Québec Declaration of Concern (Dekker et al. 2003) which postulated that worldwide abundance of anguillid eels is on the decline. In addition, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has recently recommended that the status of the American eel be considered Threatened (COSEWIC 2012). Of particular concern, American eels exhibited a precipitous decline in recruitment in the upper St. Lawrence River and Lake Ontario, to near extirpated levels, between the mid-1980s and early-1990s (Castonguay et al. 1994). Declines in eel abundance have prompted calls for a better understanding of the life cycle and status of the American eel to ensure that the species is preserved (Haro et al. 2000). Unfortunately, the life cycle of the American eel is less understood compared to other commercial fish species, owing to their complicated life cycle,

nocturnal activity, and plasticity in habitat use. For example, the estimated spawning area for anguillid eels within the Sargasso Sea, based solely on the capture of larvae, is over 2.6 million square kilometers but, to date, no adult American eels or eggs have been observed within this area (Tsukomoto et al. 2002).

Jessop et al. (2008) reviewed evidence that some yellow-stage American eels at northern latitudes exhibit seasonal migrations between saline and freshwater habitats. Eels have been captured while migrating downstream in spring using fixed traps at the outlets of Crecy Lake and Gibson Lake in Charlotte County, New Brunswick (Smith and Saunders 1955). In addition, approximately 24,000 eels were captured in Atlantic salmon smolt traps while migrating downstream in the Bec-Scie River, Anticosti Island, in early June (Caron and Raymond 1997) and 15,000 to 40,000 eels were captured using a rotary screw trap in May and June in the St. Jean River in Gaspé, Quebec (Caron et al. 2005). Similar spring runs of American eels have been identified using rotary screw traps in the Big Salmon River (Flanagan et al. 2006) and Restigouche River (Jessop et al. 2008) in New Brunswick, as well as the Margaree River in Nova Scotia (Breau et al. 2010).

It has also been reported, through interviews with local fishermen and fisheries officers, that spring downstream and fall upstream migrations of eels occur in various Nova Scotia lakes and rivers (Medcof 1969). Local fishers are aware of such runs as weirs were constructed in two different ways to capture downstream-moving fish in spring and upstream-moving fish in fall. As described in Medcof (1969) the locations of such activities include:

- the Moulin River, Grand Lake Brook, Mill Brook, and Smith Brook in Richmond County (southern Cape Breton),
- Robertsons Lake Brook, Douglas Brook, and Path Lake Brook in Queens County (south shore Nova Scotia),
- Timber Island Brook, Cox Creek Brook, and Barrington River in Shelburne County (south shore Nova Scotia), and
- Eel Brook Lake, Tusket River, Trout Brook, Argyle River, Pubnico Lake, and French Lake in Yarmouth County (south shore Nova Scotia).

Evidence of upstream annual migration of eels in scientific studies is lacking. However, Jessop (1987) identified upstream-migrating eels in the Eel River, Nova Scotia using a series of small brush and wire-netting weirs between mid-October and mid-November. Thibault et al. (2007b) used acoustic telemetry to show that yellow eels tagged in fresh water on the St. Jean River, Quebec, migrated to the estuary where they foraged throughout the summer. Although acoustic tracking activities showed that spring downstream migration occurred, the study did not continue long enough to determine whether the migrations were one-way directed migrations between saline and freshwater habitats or seasonal migrations of a recurrent nature. However, in the same study, the recapture of 15 estuary-microtagged yellow eels in fresh water one to two years following tagging suggested that the reverse migration may also occur. The purpose of such migrations has yet to be elucidated.

Clément et al. (In Press) have suggested, based on an examination of fin tissue stable isotopes, that eels in the Upper Salmon River, New Brunswick migrate seasonally from saline summer foraging grounds to fresh water for overwintering. Isotopes are variants of elements in which the number of neutrons differs. Such forms of a given element are termed "stable isotopes" if they are not radioactive and exhibit half-lives of extreme length (i.e., not experimentally measurable; Ehleringer and Rundel 1989). By examining the ratios of stable isotopes for an element in the tissues of organisms in a food web, one can derive information such as the energy source (i.e., primary producers) and nutrient pathway (i.e., trophic structure) for the food web (Vander Zanden and Rasmussen 1999). Stable isotopes of carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N) are commonly used in examining such relationships.

Isotopic ratios, or signatures, are commonly expressed as the difference between the measured isotopic ratio in a sample and a standard reference material expressed in parts per thousand (‰) using the following equation:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 10^3$$

where δX is the isotopic ratio for the element of interest (e.g. C or N), R_{sample} is the measured isotopic ratio in the sample and $R_{standard}$ is the measured isotopic ratio in the standard reference material (e.g. $^{13}C/^{12}C$ or $^{15}N/^{14}N$). The common reference material for carbon is PeeDee limestone, or belemnite, and the common reference material for nitrogen is atmospheric nitrogen (Peterson and Fry 1987). The process by which

chemical or physical reactions involved in nutrient transfer alters isotopic ratios between environmental sources, producers, and consumers at different trophic levels is termed fractionation. When the proportion of heavier to lighter stable isotopes of a given element is increased due to fractionation, this is referred to as enrichment and, in contrast, decreases in the proportion of the heavier to lighter stable isotopes is referred to as depletion.

Stable isotopes of carbon provide a good indicator of the source of nutrients (i.e., primary producers) for individuals in a food web. This is because primary producers may vary in carbon isotopic ratios, dependent on the physical availability of isotopes to the producer and/or the biased uptake of particular isotopes resulting from the carbon-fixation pathway. For example, the rate-limiting step in photosynthesis for terrestrial C_3 plants is the fixation of carbon by the enzyme ribulose bisphosphate carboxylase, or Rubisco (O'Leary 1981; Farquhar et al. 1989). C_3 plants are those which draw CO_2 directly from air during carbon fixation, in contrast to C_4 plants which draw CO_2 from the organic compound malate. Rubisco fixes carbon faster when using ^{12}C than ^{13}C and as a result, the products of photosynthesis in C_3 plants contain more ^{12}C; a chemically induced fractionation (O'Leary 1981, Farquhar et al. 1989; Raven et al. 2002). Alternatively, carbon uptake by aquatic C_3 plants is dependent on the diffusion of CO_2 in water and across the thick boundary layer of leaves (O'Leary 1981). As carbon fixation by Rubisco is no longer the rate-limiting step, both ^{12}C and ^{13}C are fixed at the same rate, physically reducing the degree of fractionation (O'Leary 1981; Raven et al. 2002).

One commonly observed pattern in nature is the distinction in carbon isotopic signatures (i.e., $\delta^{13}C$) between freshwater and marine or saline-water food webs (Hobson 1999). Freshwater food webs are generally depleted in ^{13}C compared to saline food webs (Peterson and Fry 1987, Schaffner and Swart 1991, Hobson et al. 1997). Carbon is highly depleted in ^{13}C in fresh water aquatic plants due to respired inputs of terrestrial organic matter which results in dissolved inorganic carbon with $\delta^{13}C$ values of -28‰ or lower (Rau 1978). Contrastingly, saline food webs are typically reflective of marine phytoplankton (Fry and Sherr 1984). Marine phytoplankton retrieve dissolved inorganic carbon from the surrounding water, primarily in the form of bicarbonate which has a $\delta^{13}C$ value of approximately 0‰ (Mook et al. 1974). Uptake of bicarbonate by marine phytoplankton involves a large-scale fractionation to -21 ‰ $\delta^{13}C$ (Peterson and Fry 1987). Thus, nutrient sources in saline versus freshwater food webs are typically reflective of these differences, with freshwater food webs being more depleted in ^{13}C. The carbon isotopic ratios of primary producers are retained by organisms further up the food chain, as fractionation of carbon is low (i.e., averages 0-1%) between trophic levels (DeNiro and Epstein 1978; Peterson and Fry 1987; Post 2002).

Stable isotopes of nitrogen are also enriched in saline versus freshwater food webs, although to a lesser degree (Peters et al. 1978). However, nitrogen is fractionated to a larger degree between trophic levels, averaging 3.4‰ $^{15}N/^{14}N$, such that isotopes of nitrogen are a good indicator of trophic position for organisms in a food web (Minagawa and Wada 1984, Post 2002). Used in conjunction, isotopes of nitrogen and carbon

provide a good indicator of saline versus freshwater nutrient sources and this phenomenon has been used to infer habitat use (i.e., saline vs. freshwater) of fish (Hesslein et al. 1991; Kline et al. 1998; Doucett et al. 1999).

In the Clément et al. (In Press) study in the Upper Salmon River and Point Wolfe River, New Brunswick, American eels were captured in fresh water approximately 250 m upstream of the head of saline-water intrusion ("head of salinity") in spring, summer, and fall. Tissue samples were collected from eels upon capture and analyzed in the laboratory for carbon and nitrogen stable isotopes. It was determined that most eels (69-83%) captured in spring or fall had carbon and nitrogen-enriched isotope ratios reflective of saline-derived nutrients. Although most eels had a saline signature in spring and fall, the majority of American eels captured in summer were found to have a freshwater signature. The authors suggested that American eels in the Upper Salmon River and the Point Wolfe River may be undertaking seasonal migrations between saline summer foraging and freshwater overwintering habitats, a behaviour not known to occur for eels in these rivers. Such a migration could be termed seasonal amphidromy which is defined as a migration between fresh and salt water irrespective of reproductive purposes (Myers 1949). Thus, eels captured in summer may have been those that remained to feed in fresh water whereas eels captured in spring and fall were predominately eels migrating to and from salt water, respectively. These eels were hypothesized to have retained their saline-influenced signature through winter and into spring as eels have been shown to exhibit a reduced metabolic state at low temperatures (Walsh et al. 1983).

The authors' interpretation of seasonal amphidromous migrations was supported by otolith microchemistry. Otolith microchemistry refers to the fine-scale chemical analysis of growth rings in a cross section of the otolith, an otic bone structure in fish, to measure the compositional ratios of elements of interest. During periods of growth, layers are formed in the otolith incorporating calcium and strontium ions which are available in differing ratios in fresh and salt water (Campana 1999). Although it is unknown whether incorporation of a particular ion into the otolith during growth is a result of environmental ion availability (Kraus and Secor 2004) or of salinity itself (Tzeng 1996), a positive correlation has been documented between the Sr:Ca ratio in the otolith and environmental salinity. Thus, the otolith presents a history of an eel's exposure to fresh water and salt water throughout its life for periods of growth (Shiao et al. 2006).

Using otolith microchemistry, Clément et al. (In Press) confirmed that many eels exhibiting a saline isotopic signature also displayed a record indicative of saline habitat use in the otolith (i.e., indicating growth occurring within a saline environment). However, there was no corresponding record in the otolith indicating seasonal transitions to, and overwintering in, fresh water; the habitat in which these eels were captured. Reduced growth periods in the winter may have resulted in the absence of freshwater signal in the otolith record and the authors concluded that microchemistry analysis failed to identify periods of overwintering in freshwater. Monitoring fish movements is necessary to prove the hypothesis formulated based on stable isotope analysis and otolith microchemistry. For example, Clément et al. (In Press) believed that the saline signature

observed in eels captured in fresh water was not caused by an influx of saline-derived food sources (i.e., migrating prey items) in fresh water or brief eel migrations between the estuary and freshwater environments prior capture, the authors could not fully refute these alternative hypotheses.

1.2. STUDY OBJECTIVES

A primary goal of this project was to test the hypothesis that the observed variation in isotopic signatures reported by Clément et al (In Press) was a result of eels undertaking seasonal amphidromous migrations between saline summer feeding and freshwater overwintering habitats. This was to be completed by comparing the isotopic signature of eels from the Upper Salmon River to their movements as characterized using passive integrated transponder (PIT) telemetry and coded radio transmitter tags (radio tags). Passive Integrated Transponder (PIT) tags are a useful tool in monitoring fish movements as they are low-cost and can be implanted into small fish. This technology utilizes passive radio frequency identification (RFID) which allows the tags to be activated by an external source, causing them to emit a signal indicating a unique identification code to an external receiver (Finkenzeller 2010). PIT tags have been used extensively in behavioural studies examining fish movements (Roussel et al. 2000; Linnansaari et al. 2008; Palm et al. 2009; Hering et al. 2010). However, PIT tags and stable isotopes are rarely used in conjunction (Matthews and Mazumder 2004; Cunjak et al. 2005; Hammerschlag-Peyer and Layman 2010; Speed et al. 2011). Seasonal movement patterns of yellow eels were further characterized using radio tags. Radio tags rely on an

internal power source/battery to emit coded radio signals over a long distance (>1 km) and the location of radio-tagged fish can be manually triangulated using a radio receiver and yagi antenna.

Further goals included an examination of correlations between environmental variables and eel migration in order to gain further insight into which factors may influence migration. Finally, to aid in evaluating the current and future status of migrating American eels in the Upper Salmon River, run characteristics were examined including the physical characteristics and enumeration of migrating eels, as well as the efficiency of capture mechanisms including rotary screw traps (RSTs) and fyke nets to improve future run-characterization studies.

1.3. STUDY AREA

The Upper Salmon River (45º36'N, 64º56'W) is located in southeastern New Brunswick, Canada and flows along the eastern edge of Fundy National Park (Figure 1.1). The Upper Salmon River watershed encompasses an area of 177 km^2. The river flows into the Bay of Fundy which is noted for its extreme tidal fluctuations. The lowest 1.5 river kilometers (rkm), of the Upper Salmon River, from the mouth of the river to the limit of salt penetration (i.e., head of salinity) is subject to these tidal fluctuations and, for the purposes of this study, is considered the estuary. These semi-diurnal fluctuations in the area of the study site averaged 8.3 vertical metres and ranged between 5.3 and 11.0 m in 2009 and 2010 according to the Canadian Hydrographic Service (CHS) database for

Herring Cove, New Brunswick. At low tide, the estuary consists of shallow, freshwater channels with predominately sand and gravel substrate bordered by tidal flats. Water surface area doubles between low tide and high tide and at high tide salinity in the estuary is upwards of 29 ppt. Above the head of salinity, the subsequent 8 rkm of the main stem is characterized by predominantly fast-flowing and boulder-strewn habitat.

1.4. DOCUMENT STRUCTURE

This thesis has been written in article format and is divided into five chapters. Chapter 1 is a general introduction to the project including relevant background information and the goals of the study. Chapters 2 through 4 present collected data and have been written in article format according the requirements of target journals. Chapter 5 is a general discussion that synthesizes the findings of Chapters 2 through 4 and proposes directions for future research.

Chapter 2 examines the relationship between seasonal movements of individual eels and their corresponding stable isotopic signatures to determine whether eels are undertaking seasonal amphidromous migrations between saltwater summer foraging and freshwater overwintering habitats and if these movements are driving the observed variation in isotopic signature observed by Clément et al. (In Press). Movements of individual eels were examined using passive integrated transponder telemetry and radio transmitter telemetry coupled with both fixed-station and manual tracking methods.

This paper, titled, "**Correlation of seasonal movement pattern and stable isotopic signature in the American eel as determined using passive integrated transponder and radio telemetry: freshwater residency vs. seasonal amphidromy**" will be submitted to *Oecologia* for consideration.

Authors: Sweezey, M.J., Clément, M. and Courtenay, S.C.

Chapter 3 examines correlations between environmental variables and seasonal amphidromous migrations of yellow-stage American eels in the Upper Salmon River. The timing of migration for individual eels was determined using both daily rotary screw trap (RST) capture and passive integrated transponder telemetry. A fixed antenna array was maintained near the head of salinity to record downstream and/or upstream migrations of individually tagged eels between saline and freshwater habitats and these records were examined with respect to various environmental parameters hypothesized to affect eel migratory behaviour.

This paper, titled, "**Environmental correlates of amphidromous migration by yellow-stage American eels (*Anguilla rostrata*) in the Upper Salmon River, New Brunswick, Canada**" will be submitted to *Journal of Fish Biology* for consideration.

Authors: Sweezey, M.J., Courtenay, S.C. and Clément, M.

Chapter 4 has been compiled as a manuscript for Canadian Technical Reports of Fisheries and Aquatic Sciences and examines the run characteristics of downstream-migrating yellow-stage American eels in spring. The goal of this report was to present

information on the status of migrating American eels in the Upper Salmon River including physical characteristics and abundance estimates. In addition, the capture efficiencies of various trap methods including a rotary screw trap (RST), which is widely used in long-term monitoring programs for various migrating fish species, were determined in order to aid in the development of potential long-term monitoring programs examining migrating American eels.

This report, titled, "**Run-size quantification and biological characteristics of spring-migrating yellow-stage American eels (*Anguilla rostrata*) in the Upper Salmon River, New Brunswick, in 2009 & 2010**" will be submitted to *Canadian Technical Reports of Fisheries and Aquatic Sciences* for consideration.

Authors: Sweezey, M.J., Clément, M. and Courtenay, S.C.

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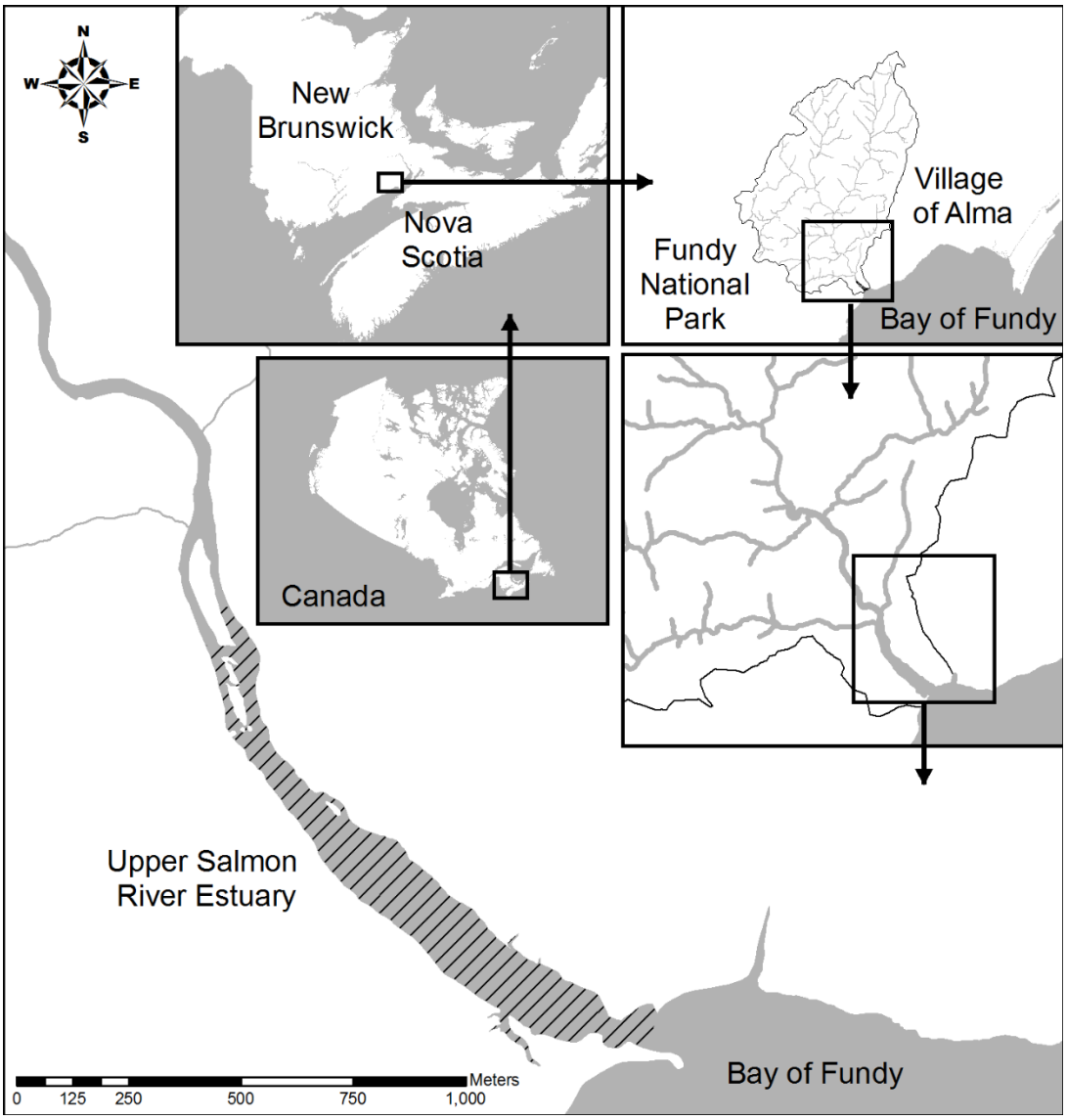

Figure 1.1. Map of the project study site; the main stem of the Upper Salmon River in New Brunswick, Canada.

2. Correlation of seasonal movement pattern and stable isotopic signature in the American eel as determined using passive integrated transponder and radio telemetry: freshwater residency vs. seasonal amphidromy

2.1. ABSTRACT

Previous research has shown that some yellow-stage American eels captured in fresh water in the Upper Salmon River, New Brunswick, Canada, in spring and fall exhibit carbon and nitrogen stable isotopic signatures that suggest saline-derived diets. This led to the hypothesis that eels exhibiting saline isotopic signatures may migrate seasonally between saline summer foraging and freshwater overwintering habitat, thus accounting for the presence of saline-signature eels in fresh water in spring and fall. The goal of the current study was to test this hypothesis using passive integrated transponder (PIT) and radio telemetry. In total, 288 eels were PIT tagged and tested for stable isotope analysis upon capture in the spring of 2009 or 2010. Habitat transitions of PIT tagged eels were monitored using a flatbed antenna array installed near the head of salinity and habitat use in the estuary was determined using a portable tag detector at low tide. Throughout the study period, the antenna array identified 74% of all PIT tagged eels which were released in fresh water 600 m upstream of the array in the springs of 2009 and 2010. PIT antenna array data indicated two periods of directed movement in spring-early summer and late

summer-fall and two periods of minimal movement were identified in summer and winter. The spring-summer migration was downstream-directed as all eels were released upstream of the antenna array indicating downstream movement. In addition, portable PIT antenna surveys of the estuary in the summers of 2009 and 2010 confirmed that 36% and 34% of tagged eels, respectively, migrated downstream of the antenna prior to detection. The summer-fall migration was determined to be upstream-directed as 80% of eels identified in the estuary in the summer of 2009 were identified by the antenna array in fresh water during that period. Radio tracking supported these conclusions as interhabitat transitions of radio-tagged eels during the spring-summer and summer-fall migration period were exclusively downstream and upstream directed, respectively. Significantly higher proportions of eels displaying a saline isotopic signature upon capture were identified migrating to the estuary during the spring-summer migration, residing within the estuary during summer, and migrating to fresh water during the summer-fall migration. These findings suggest that the spring and fall presence of yellow eels in the Upper Salmon River with saline isotopic signatures results from seasonal migrations of eels between saline foraging and freshwater overwintering habitat. The annual seasonality of migrations were further confirmed as 21% (33/154) of eels PIT tagged in 2009 were again detected during the spring-summer migration period of 2010. Inferences of habitat use based on otolith microchemistry or stable isotope analysis should be made with caution because habitat use during periods of low growth may be undetectable in elemental records.

2.2. INTRODUCTION

The American eel, *Anguilla rostrata*, is one of the most widely distributed fish species in eastern North America and the Western North Atlantic, and an integral component of ecosystems within its range (Tesch 2003; COSEWIC 2012). The American eel is particularly important to aboriginal peoples and provides commercial and recreational fisheries in Canada with annual harvests ranging between 500 and 1200 t between 1961 and 2003 (DFO 2010). However, harvests have declined from approximately 1100 t in the late 1980s to approximately 500 t in 2003 and the estimate for 2007 places annual harvest at 459 t (DFO 2010). Most eel fishing in Canada has historically occurred in the St. Lawrence River system and in tidal waters of the Gulf of St. Lawrence (Cairns et al. 2008). Recent studies have shown that worldwide abundance of anguillid eels, including the American eel, is in decline (Haro et al. 2000; Dekker et al. 2003). The status of the American eel is of particular concern, as its abundance in the upper St. Lawrence River and Lake Ontario, Canada, declined precipitously between the mid-1980s and early-1990s to near extirpation levels (Castonguay et al. 1994; Casselman et al. 1997). As a result, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recommended in 2012, that the American eel be designated as Threatened (COSEWIC 2012). Unfortunately, many facets of the American eel's life cycle remain poorly understood. For example, recent studies using otolith microchemistry have shown that American eels are not an obligate catadromous species, as previously believed, but that various life history patterns occur, including complete saline or freshwater residency and

inter-habitat shifting in which transitions between saline and fresh water are exhibited at some point in the continental life cycle (Daverat et al. 2006; Lamson et al. 2006; Thibault et al. 2007a; Jessop et al. 2008).

The yellow stage of the American eel life cycle is the feeding and growth stage, and ranges between 5 and 40+ years duration in Atlantic Canada (Jessop 1987). Consequently, yellow-stage American eels face a long period of anthropogenic stressors, including fisheries, habitat alteration, and contaminant bioaccumulation (Haro et al. 2000; COSEWIC 2012). Barriers to migration (e.g., dams, improperly installed culverts) may be detrimental to yellow stage eels where migration between saline and freshwater habitat is required. Identifying seasonal habitat use and movements of yellow-stage American eels will enable managers to make informed decisions relating to habitat protection for the conservation of this species.

One way to study fish habitat use is through stable isotopes. Stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are distinctly enriched in saline vs. freshwater food webs (Fry and Sherr 1984; Peterson and Fry 1987). Studies have capitalized on this difference to identify large-scale movements of fish across salinity boundaries (Hesslein et al. 1991; Kline et al. 1998; Doucett et al. 1999). This is possible because organisms retain the isotopic signature derived from their prey for a period dependent on the turnover rate of elements in tissue (Tieszen and Boutton 1988). However, few studies have examined how the movements of individual fish relate to their respective isotopic

signatures (Matthews and Mazumder 2004; Cunjak et al. 2005; Hammerschlag-Peyer and Layman 2010; Speed et al. 2011).

A recent study examining the isotopic ratios of carbon and nitrogen in yellow-stage American eels captured in the Upper Salmon River and Point Wolfe River, New Brunswick, found that some eels captured above the head of tide in fresh water exhibited isotopic signatures reflective of freshwater food webs whereas others exhibited isotopic signatures reflective of saline food webs (Clément et al. In Press). Furthermore, the proportion of eels exhibiting freshwater vs. saline isotopic signatures varied temporally, such that between 69% and 90% of the eels captured in fresh water during the spring and fall had a saline isotopic signature whereas 85% to 93% of eels captured in fresh water during the summer had a freshwater isotopic signature. It was hypothesized that a proportion of American eels in these rivers migrate seasonally from saline summer foraging grounds to freshwater overwintering habitat. However, due to several factors, including the proximity of the capture location to the estuary, it could not be determined whether influxes of saline-derived food sources (i.e., migrating prey items) vs. migration pattern of the eels themselves were responsible for the observed variability of isotopic signatures.

Seasonal migrations of yellow eels between saline summer foraging and freshwater overwintering habitats can be described as seasonal-amphidromous migrations. Amphidromy is a form of diadromy, whereby fish migrate between fresh water and salt water irrespective of reproductive purposes (Myers 1949). Evidence of seasonal-

amphidromous yellow-stage American eels has been documented at northern latitudes through interviews with local fishers in Nova Scotia, Canada (Medcof, 1969), and through studies which have examined migrating yellow eels (Smith and Saunders 1955; Jessop 1987, Thibault et al. 2007b). However, the dynamics and ultimate purpose of this migration pattern remain poorly understood and the geographic extent over which American eels exhibit amphidromous migrations of this nature is unknown (Jessop 2008). Otolith microchemistry analyses of eels captured in varying habitats, suggest that most eels captured in saline habitats display a resident microchemical signature (Lamson et al. 2006; Jessop et al. 2008). However, it has been hypothesized that overwintering habitat use may be missing from otolith records (Thibault et al. 2007; Jessop 2008; Clément et al. In Press) due to a reduced metabolic rate exhibited by American eels in winter (Walsh et al. 1983). Therefore, the importance of freshwater habitat to eels exhibiting saline isotopic or microchemical signatures will be underestimated if such eels migrate to freshwater habitat for overwintering.

The goal of this study was to test the hypothesis of Clément et al. (In Press) that eels undertake seasonal amphidromous migrations from saline habitat to freshwater habitat for overwintering and that freshwater captured eels exhibiting saline isotopic signatures in spring and fall undertake such migrations, whereas those exhibiting freshwater isotopic signatures are year-round residents in fresh water. To test this hypothesis, the Upper Salmon River was selected and we tracked fish movements using passive integrated transponder (PIT) tags and coded radio transmitter tags (radio tags) and compared

seasonal movement patterns of individual eels with their isotopic signature measured upon initial capture and tagging in fresh water. PIT tags and radio tags are used for tracking fish movements. Fish tracking and stable isotope analysis have only recently been used in conjunction to characterize fish movement and foraging patterns (Cunjak et al. 2005; Bergstad et al. 2008; Cooke et al. 2008; Hammerschlag-Peyer and Layman 2010; Speed et al. 2011).

2.3. METHODS

2.3.1. Study Area

The Upper Salmon River (45º36'N, 64º56'W) drains 177 km^2 of southeastern New Brunswick, Canada, where it forms the eastern border of Fundy National Park (Figure 2.1). For the purposes of this study, the lowest 1.5 river kilometers (rkm), from the mouth to the limit of salt penetration (i.e., head of salinity), was considered the estuary. This estuary drains into the upper Bay of Fundy, which is locally subject to macrotidal semi-diurnal fluctuations averaging 8.3 vertical metres (range 5.3-11.0 m, data from the Canadian Hydrographic Service (CHS) for Herring Cove, New Brunswick). At low tide, the estuary consists of shallow, freshwater channels bordered by tidal flats. Channel substrates consist primarily of a sandy to gravely mixture covered in a fine layer of silt. Water surface area doubles between low and high tide and at high tide salinity in the estuary is $\geq$29 ppt. Above the head of salinity, the subsequent 8 rkm of the Upper Salmon's main stem is steep (mean slope 10.9%), predominantly fast-flowing, and boulder-strewn. Yellow eels in the main stem are restricted from moving into tributaries

by waterfalls (Figure 2.1). Geospatial calculations were completed using ArcGIS 9.3 SP1 (ESRI Inc., Redlands, CA), data sets from the New Brunswick Aquatic Data Warehouse (Canadian Rivers Institute, Fredericton, NB, Canada), and an ASTER Global Digital Elevation Model provided by NASA's Land Processes Distributed Active Archive Center.

2.3.2. Sample Collection

Passive Integrated Transponder Tag Sample Collection

Yellow-stage American eels were captured in fresh water using a 1.52 m rotary screw trap and two fyke nets with 10 mm mesh wings and body and a 6 mm mesh bag installed 250-300 m upstream of the head of salinity and set to target downstream-moving fish (Figure 2.1). Capture periods were May 5 - July 3, 2009 and April 29 - June 18, 2010. Capture periods ended in both years when the last five days of full operation (i.e., all three traps) captured no more than 5% of the total catch. Captured American eels were anaesthetized in a 250 ppm solution of tricaine methanesulphonate (MS-222; Argent Laboratories, Redmond VA) and water until a state of immobility was observed, then weighed in air and measured for total length. A tissue sample was then incised from the edge of the right pectoral fin for stable isotope analysis using a pair of sanitized surgical scissors. A 23 mm glass-encapsulated passive integrated transponder (PIT) tag [Texas Instruments (TIRIS^{TM}) model RI-TRP-RRHP, 134.2 kHz] was surgically implanted into the abdominal cavity following the protocol of Roussel et al. (2000). The incision area was sealed using a single drop of n-butyl cyanoacrylate (Vetbond^{TM} surgical glue) to

reduce tag loss and promote healing. Only eels ≥25 cm in length were tagged, which limited tag weight to <4% of eel weight. Approximately 20% and 17% of American eels tagged in 2009 and 2010, respectively, were held in live boxes for 10 days prior to release to determine tag retention and handling mortality. Tag retention was 100% and no adverse effects relating to tagging were identified with the exception of four eels that were immediately euthanized during tagging due to surgical complications. All other captured eels were released on the day of tagging, and no more than two days following capture. Eels captured one to two days prior to the day of tagging were held in live boxes in the same manner as control-holds. All tagged eels were released in fresh water, 800 m upstream of the head of salinity (i.e., 2.3 rkm; Figure 2.1). All procedures were carried out according to the Canadian Council on Animal Care guidelines and were approved by the Animal Care Committee of both the University of New Brunswick (Protocol #09043/10003) and Fisheries and Oceans Canada Maritimes Region (Protocol #09-11).

Coded Radio Transmitter Telemetry Sample Collection

Coded radio transmitters were surgically implanted into the abdominal cavities of 27 yellow-stage American eels in 2009. Eels were captured in four different periods using an RST, fyke nets, or electrofisher (Table 2.1). Nine of the implanted eels were captured between May 22 and June 22, 2009, during sample collection activities for the passive integrated transponder study using the RST and fyke nets in fresh water. Two types of Lotek radio transmitters (Lotek Wireless Inc., Newmarket, Ontario, Canada) were implanted including NTC-6-1 tags (22.4 mm long, 9.1 mm diameter, 2.8 g in air, battery

life of 232 days with a burst rate of 5 s) and NTC-3-2 tags (15.5 mm long, 4.5-6.5 mm diameter, 1.1 g in air, battery life of 124 days with a burst rate of 10 s). A maximum tag to fish weight ratio of 3.9% was maintained throughout the study. Most captured eels were too small to be fitted with the NTC-6-1 tags; hence the smaller NTC-3-2 tags were used later in the study period. Captured eels were anaesthetized, measured, and weighed in the same manner as PIT tagged eels. The incision area for coded radio transmitter tags was located on the posterior portion of the abdomen, a sufficient distance anterior to the anus so that the intestinal loop would not protrude upon incision (i.e., approximately 15-30 mm depending on eel size). To prevent infection, the incision area was swabbed with iodine prior to surgery and a 15 mm incision was made using a sterilized scalpel. The radio transmitter was inserted anteriorly and a separate exit hole was created for the antenna wire through the lateral abdominal wall using a sterilized piercing needle through which the wire was fed. Once the piercing needle was removed, the incision was stitched using three synthetic sutures. All procedures were carried out according to the Canadian Council on Animal Care guidelines and were approved by the Animal Care Committee of both the University of New Brunswick (Protocol #09043/10003) and Fisheries and Oceans Canada Maritimes Region (Protocol #09-11). Tagged eels were held in a live box for a minimum of 48 hours prior to release. Tagged eels were released in the vicinity of their capture location in all cases, with the exception of the nine eels implanted in spring which were released upstream of the capture area with PIT tagged eels at approximately 2.3 rkm.

2.3.3. Tracking Data Collection

Passive Integrated Transponder (PIT) Telemetry

To monitor transitions of PIT tagged American eels between saline and freshwater habitats, a flatbed PIT antenna array and system (Technologie Aquartis) was installed in fresh water near the head of salinity and operated for periods ranging between June 10 to October 27 in 2009 and a shortened period of May 12 to August 2 in 2010. The array consisted of four elongated rectangular antennae (1m x ~15 m) sitting flat on the river bottom in an end-to-end fashion so that the entire width of the river (~60 m) was monitored for fish passage. The system operated 24 hours a day throughout the installed periods with the exception of 3 and 4 days of interruption in 2009 and 2010, respectively, due to preventative maintenance or technical difficulties. It was found in 2009 that two of the antennae were under saline water influence during spring tide events. Because saline water reduced the detection range of the antennae to as low as 0.2 m during these events, the system was moved 200 m upstream in 2010 (Figure 2.1). With the exception of periods of saline water intrusion, the detection range of the antenna array varied between 0.5 and 1.5 m. Full detection coverage of the water column was not maintained throughout operation, particularly during periods of high discharge which corresponded to increased depth. The antenna detection rates for the spring of 2009 and 2010, respectively, were estimated at 75 and 79%. These estimates were based on the number of eels that were released upstream of the antenna array following array installation in spring that were subsequently identified within the estuary during the summer of that

year (via methods described below). As 100% of these eels moved past the antenna between release and identification in the estuary, the detection rate was the percentage of eels that the antenna detected during passage and was similar between years.

Saline water, characteristic of estuaries, attenuates radio signals and strongly diminishes the reading range of PIT tags (Niezgoda et al. 1998). However, the estuary of the Upper Salmon River provided a unique circumstance in which PIT telemetry could be used to detect the presence of tagged fish due to the extreme tidal fluctuations of the Bay of Fundy. During low tide, saline waters withdraw from the Upper Salmon estuary, leaving a freshwater channel with large areas of exposed substrate. The low-tide channels, therefore, present conditions of low conductivity in which PIT tagged fish are detectable. A portable PIT tag detection unit (Leonie RFID Mobile System, Technologie Aquartis) was used to conduct searches in the estuary at low tide and locate tagged eels. The system consisted of a 60 cm diameter antenna ring attached to the end of an adjustable fiberglass handle to a backpack-enclosed module powered by a 12-V DC battery. A small monitor extended from the backpack which signaled tag detection by an audible cue and displayed the identification number of the detected tag. Upon identifying an individual, its location was recorded using a global positioning system (GPS) accurate to between 5 and 15 m. The estuary was surveyed between August 10 to August 28, in 2009, and June 24 to July 19, in 2010, to identify eels residing in estuarine waters. Perpendicular transects of the estuary were completed at low tide starting at the mouth of the river by sweeping the portable antenna ring back and forth, thus monitoring a width

of approximately 5 m with each transect. An assistant measured and marked the 5 m transects on the river banks using flagged rebar to ensure that all available habitat was searched. A total area of 147100 m^2 was surveyed in 2009 including exposed substrate at low tide (i.e., mud flats) to determine if eels were seeking refuge by burrowing within moist substrate, a behaviour known to occur by yellow eels in winter at northern latitudes (Smith and Saunders 1955; Cairns et al. 2012; Tomie 2013). Based on the observed habitat use in 2009, a reduced area of 74,200 m^2 was surveyed in 2010 which consisted only of areas wetted at low tide (i.e., low-tide channels).

Coded Radio Transmitter Telemetry

Radio tracking was conducted on foot during daytime at low tide using a Lotek SRX-600 receiver/datalogger (Lotek Wireless Inc.) and a 150 Mhz handheld yagi antenna. The detection range of the transmitter tags, in fresh waters of the study area, varied between 300 m and >1 km. Tracking was conducted by walking adjacent to the low tide channels in the estuary or by walking a riverbank footpath above the head of tide. The antenna was pointed towards the river at all times. Regular tracking events covered an area from the river mouth (i.e., 0 rkm) to the location of the eel believed to be furthest upstream (i.e., ranging between 2.3 to 3.2 rkm; Figure 2.1). As with PIT tracking, radio tracking of the estuary was also possible due to the prevalence of fresh water at low tide. Signals were triangulated so that the location of a tagged eel could be identified within 1 m accuracy. Locations were recorded using a global positioning system (GPS) accurate between 5 and 15 m. Regular radio tracking events were conducted 3 to 5 days weekly

between May 22 - August 21 and September 15 - 25 2009, followed by approximately two regular tracking events per month between October 2009 and March, 2010. To determine if tagged eels were present upstream of the regular tracked area, a complete tracking event of the entire area of the river accessible to radio-tagged eels (i.e., between 0 and 8.6 rkm; Figure 2.1) was completed in summer (August 4) and winter (December 18) of 2009. It was determined that no tagged eels were present upstream of the normal tracked area during complete tracking events.

Radio transmitter tags may have adversely affected some eels as one was found dead on the river bank on August 4, 2010 and the cause of death appeared to be agitation of the exit hole through which the radio antenna protruded as the exit hole was widened and surrounding tissue appeared necrotic. However, the majority of eels made clear seasonal large-scale and short term small-scale movements indicating some degree of good health.

2.3.4. Stable Isotope Analysis

Collected tissue for stable isotope analysis was stored in 99% ethanol or immediately frozen or dried when possible. Storage in ethanol is a preferred field preservation method in that tissue samples do not require immediate freezing or drying. To determine if storage in ethanol altered the resulting isotopic values, duplicate pectoral fin tissue samples were collected from 27 fish by dividing samples in half and freezing one portion immediately while storing the other portion in ethanol. In addition, to determine if isotopic values of fin tissue differed from muscle tissue, 20 American eels, sacrificed in a previous study wherein caudal fin tissue was analyzed for $\delta^{13}C$ and $\delta^{15}N$ values

(Clément et al. In Press) were used for pectoral fin and muscle tissue comparison. White muscle tissue in fish has been found to be the least variable tissue in δ^{13}C and δ^{15}N and, therefore, is the best tissue for isotope comparisons in ecological studies (Pinnegar and Polunin 1999). However, the collection of muscle tissue requires lethal fish sampling and, therefore, fin tissue sampling is preferred. The samples, all collected between 2005 and 2007 in the same capture location as the current study, were thawed and pectoral fin and muscle tissue were collected for comparison. Pectoral fin tissue was collected in the same manner as described above whereas muscle tissue was incised from the left flank at the dorsal fin origin using a scalpel.

All samples were analyzed for δ^{13}C and δ^{15}N at the Stable Isotopes in Nature Laboratory (SINLAB) of the Canadian Rivers Institute, University of New Brunswick, Fredericton, New Brunswick. Collected tissue was oven-dried at 60°C for 48 hours. Once dry, muscle tissue was ground using a mortar and pestle. Approximately 0.2-0.3 g of ground muscle tissue or pieces of dried fin tissue were weighed in tin cups, then analyzed using a Carlo Erba NC2500 Elemental Analyzer (Milan, Italy) coupled to a continuous flow Thermo-Finnigan Delta Plus or Delta XP mass spectrometer (Bremen, Germany). Results are expressed as per mil ratios (‰) of the measured isotope values relative to PeeDee Belemnite carbonate (PDB) and atmospheric nitrogen (AIR) standards for δ^{13}C and δ^{15}N, respectively. Analytical error throughout the course of the study was determined to be $\leq$0.1‰ for δ^{13}C and <0.4‰ for δ^{15}N values, respectively, based on within-run replicates of internationally accepted (IAEA) standards.

2.3.5. Data Analyses

Passive Integrated Transponder Data Analyses

Tracking data were used to classify eels as exhibiting any of four groups of seasonal movement: Freshwater Residency, Spring-Summer Migration, Saline Residency, and Summer-Fall Migration. Eels with no associated telemetric data were termed Unclassified. Five classification rules were applied to group individuals into each of the four behavioural groups (Table 2.2). Three groups reflected movement patterns characteristic of seasonal amphidromy (Spring-Summer Migration, Saline Residency, Summer-Fall Migration groups) and one group reflected a movement pattern characteristic of freshwater residency (Freshwater Residency group). The classification rules were applied in order of the best evidence that an eel exhibited a particular movement pattern (e.g., manual tracking of an eel's real-time location being the best evidence of residency in freshwater or saline habitat). When an individual eel was first classified in one of three amphidromous groups, that eel could not subsequently be classified in the freshwater residency group, or vice versa, as a subsequent rule would provide weaker evidence than that which designated the preceding classification. However, the amphidromous groups are not mutually exclusive as an amphidromous eel would exhibit all three movement patterns in a given year.

Rule #1 dictates that tagged eels found inhabiting the estuary by portable antenna survey in the summer of release were classified in the Spring-Summer Migration group as well as the Saline Residency group. Rule #2 dictates that tagged eels detected $\geq$4 nights in the

year of release by the fixed antenna array were classified in the Freshwater Residency group, as high frequency of detections were indicative of prolonged freshwater activity. If an eel was identified in the estuary per Rule #1, it could not be included within this grouping having been previously classified in an amphidromous group (i.e., Saline Residency). Four behavioural periods (Spring-Summer Migration, Summer Residency, Summer-Fall Migration, and Winter Residency) were defined based on seasonal dynamics of eel movement characterized by the PIT antenna array. These periods were used in the development of the following rules and further described in the Results section. Rule #3 dictates that eels detected at the antenna array during the Summer Residency period were classified in the Freshwater Residency group as such eels were utilizing freshwater habitat during a period devoid of mass directed movement. Rule #4 dictates that eels detected at the antenna array during the Spring-Summer Migration period of mass directed movement were classified in the spring migration group. Finally, Rule #5 dictated that eels detected at the antenna array during the Summer-Fall Migration period of mass directed movement were classified in the Summer-Fall Migration group.

Statistical Analyses

We used paired t-tests to determine if significant differences in δ^{13}C and δ^{15}N values existed between tissue types or resulted from tissue storage in ethanol. If significant, a linear regression and subsequent t-test for equality of slope (i.e., 1:1) was applied to determine if a constant value, or regression equation, needed to be applied as the correction factor. Appropriate correction factors were then applied so that final corrected

values were representative of pectoral fin tissue frozen, or dried, immediately following collection.

To identify groups of American eels exhibiting distinctive and contrasting isotopic signatures, we used SAS 9.00 (SAS Institute Inc., Cary, NC, USA) to perform a centroid linkage cluster analysis using δ^{13}C and δ^{15}N values of American eels PIT tagged and radio-tagged in the springs of 2009 and 2010. To determine the best number of clusters that described the dataset, three stopping rules, the Cubic Clustering Criterion (Sarle 1983), the Pseudo t^2 statistic (Duda and Hart 1973), and the Calinski and Harabrasz Pseudo *F*-statistic (Calinski and Harabasz 1974) were employed as they were found in a simulation study to perform best among 30 tested methods (Milligan and Cooper 1985).

Between-cluster and between-year group comparisons of mean length and mean weight were completed using *t*-tests. To determine if significant differences in movement patterns existed between cluster-grouped eels, between-cluster group comparisons of the proportion of tagged American eels exhibiting each of the four movement groups were completed using Fisher's exact test. In addition, to determine if δ^{13}C and δ^{15}N values could be used to predict whether an eel would exhibit freshwater resident or amphidromous movement tactics, a canonical linear discriminant analysis was used with two groups. The first group consisted of all eels most likely to be freshwater residents (i.e., eels classified in the Freshwater Residency group) and the second group consisted of all eels most likely to be amphidromous migrators (i.e., eels classified in the Spring-Summer Migration, Saline Residency, and Summer-Fall Migration groups). All

statistical analyses, unless otherwise specified, were completed using STATA 11.1 (StataCorp LP, College Station, TX, USA) or SigmaPlot 11.0 (Systat Software Inc., Point Richmond, CA, USA) and a critical significance level of P=0.05 was used in all cases.

Coded Radio Transmitter Data Analyses

To examine the seasonal movements of radio-tagged eels with respect to river distance, GPS positions were converted to lineal river distance values (i.e., rkm; distance from the river mouth in kilometres) using the Network Analyst extension in ArcGIS 9.3 SP1 (ESRI Inc., Redlands, CA, USA) and a stream shapefile provided by the New Brunswick Aquatic Data Warehouse (Canadian Rivers Institute, Fredericton, NB, Canada). Tracking data were divided into four behavioural periods based on patterns of seasonal movement of PIT tagged eels: Spring-Summer Migration, Summer Residency, Summer-Fall Migration, and Winter Residency. Eels that were not identified during a regular tracking event, were considered to have moved beyond the mouth of the river, where they could not be detected due to distance and/or saline attenuation of radio signals. This conclusion was drawn for a number of reasons. Firstly, disappearance of tagged eels was most common for individuals identified migrating downstream towards the estuary prior to disappearance, or for eels utilizing the estuary in summer. Secondly, eels that disappeared from the regular tracked area were not identified upstream during complete-river tracking events in the summer and early winter of 2009. Finally, signal testing of tags in the estuary was completed at low tide on August 11, 2010. Radio tags were randomly placed in water at the surface of the substrate in twenty locations including

low-tide channels and puddles which were isolated from flowing water. A second person attempted to detect a signal from the placed tags from the shore at a distance >100 m. A 100% detection rate was found for the low-tide channels (18 locations tested). However, no signal could be detected from tags placed in two small tidal puddles with salinity >20 ppt which were isolated on exposed sandbars.

2.4. RESULTS

2.4.1. Passive Integrated Transponder Study

Stable Isotope Results

A total of 154 and 134 eels were captured, PIT tagged, tissue-sampled, and released in the springs of 2009 and 2010, respectively. In addition, nine eels of sufficient size for radio tag implantation were captured, tissue-sampled, and radio-tagged during the 2009 spring sampling period (isotope results included here). Collectively, stable isotope analysis identified a similar pattern to that described by Clément et al. (In Press) for spring-captured eels in the Upper Salmon River with δ^{13}C values ranging between -27.36‰ and -9.38‰ and δ^{15}N ranging between 7.03‰ and 15.52‰ (Figure 2.2). After performing a centroid linkage cluster analysis to δ^{13}C and δ^{15}N values from pooled individuals (n = 297), clustering at the level of two groups was determined to best represent the dataset due to a local peak in Cubic Clustering Criterion values, a high Pseudo-F value, and a low Pseudo t^2 value relative to the value for the next cluster fusion. The cluster groups were clearly distinguished based on δ^{13}C with a between-group

transition point of approximately -18‰ to -19‰. The group with more negative $\delta^{13}C$ values is characteristic of eels feeding in freshwater food webs (depleted ^{13}C), whereas the group enriched with ^{13}C is characteristic of eels feeding in saline food webs (Harrod et al. 2005). Stable isotopes of nitrogen have also been found to be enriched in saline versus freshwater food webs (Peters et al. 1978). Therefore, the ^{13}C and ^{15}N depleted cluster group was termed the Freshwater Signature Group (FWS) and the ^{13}C and ^{15}N enriched cluster group was termed the Saline Signature Group (SAS) (Figure 2.2).

Between-year and between-cluster group comparisons identified that the eels captured in the spring of 2009 had a significantly higher mean $\delta^{15}N$ than those captured in the spring of 2010 (*t* test, $P < 0.05$; Table 2.3). No other differences were identified.

Telemetry Results

Distinct trends were identified relating to the number of nights individual eels were detected at the antenna array (Figure 2.3). A small number of eels (16) were detected on consecutive nights ($\geq$4 nights) and were therefore considered to be resident to the immediate area of the antenna array. The activity of these eels was considered separately to aid in distinguishing behavioural periods of non-resident eels using their observed movements. A period of increased directed movement was observed in the spring and early summer of 2009 between June 10, the date of antenna array installation, and June 29, after which activity markedly declined. Generally, movement in this period was characterized as pass-through detections on a single night and was termed the Spring-

Summer Migration Period. Movement during this period was considered directed downstream as all eels were released from a known location upstream prior to detection. The period of low activity that followed was termed the Summer Residency Period as mass directed movement was not observed during this time period. The Summer Residency Period continued until August 30, when a second period of mass directed movement occurred marking the onset of the Summer-Fall Migration Period. This event was considered directed upstream movement as 80% (43/54) of eels identified in the estuary during the summer of 2009 were detected while undertaking mass directed movement during this period. The Summer-Fall Migration Period slowed to a complete cessation following October 17, marking the onset of the winter residency period. Cessation of directed movement continued until removal of the antenna array on October 27; and the period following antenna removal was further characterized as a period of reduced activity through radio tracking of select individuals. A similar pattern was again observed in 2010 when, upon installation of the antenna array, eels released 600 m upstream in 2010, as well as 21% (33/154) eels tagged in 2009 were detected while making mass directed movement across the antenna array. This peak in directed movement (i.e., the Spring-Summer Migration Period of 2010) declined until July 2, after which movement continued to be infrequent for the period leading to removal of the antenna array on August 2 (i.e., the Summer Residency Period of 2010). Less movement was observed during summer at the antenna array in 2010, which was installed approximately 200 m upstream of its 2009 location.

The portable PIT antenna survey of the estuary during the Summer Residency Period of 2009 identified 36% (55/154) of PIT tagged eels. All eels detected by portable antenna were utilizing available cover in the low-tide channels which ranged from dense mats of sea lettuce (*Ulva intestinalis*) in the lower 1 rkm to primarily boulder and rock-cover closer to the head of salinity (Figure 2.4). Typical substrate (i.e., sand/gravel) in the estuary was not found to attenuate the signal of PIT tags as tags experimentally buried up to 20 cm could still be detected by the manual detector. No eels were identified burrowed within the substrate that was exposed at low tide and no burrows were visually identified during tracking activities. Similarly, in the Summer Residency Period of 2010, the portable antenna detected 34% (46/134) of PIT tagged eels released in the spring 2010 as well as 23% (36/154) of PIT tagged eels released in the spring of 2009. A similar pattern in habitat use to that identified in the previous year was observed.

Telemetric data in the year of release were collected for 71% (109/154) of eels PIT tagged in 2009 and 74% (99/134) PIT tagged in 2010. Using the classification rules for 2009 data, 10 eels were classified as exhibiting freshwater resident behaviour (i.e., 10 eels in the Freshwater Residency Group), whereas 99 eels were classified as exhibiting amphidromous behaviour (i.e., 54 eels in the Saline Residency Group, 78 in the Spring-Summer Migration Group, and 75 in the Fall Migration Group). A similar pattern was observed in 2010, as 5 eels were classified as exhibiting freshwater resident behaviour (i.e., 5 eels in the Freshwater Residency Group), and 94 eels were classified as exhibiting

amphidromous behaviour (i.e., 46 eels in the Saline Residency Group, and 94 in the Spring-Summer Migration Group).

Isotope and Telemetry Comparisons

One eel in 2009 and three eels in 2010 belonging to the FWS isotopic cluster grouping were identified by portable antenna survey in the year of release. All FWS eels were found concentrated near the head of salinity (Figure 2.4). In contrast, 54 eels in 2009 and 43 SAS eels identified by portable antenna survey in the year of release were found concentrated in the estuary between 0 and 1 rkm; an area in which no FWS eels were identified.

Between-cluster group comparisons (i.e., FWS vs. SAS eels) of the proportion of eels exhibiting telemetry-classified behaviours yielded significant differences in all cases (Fisher's exact test, $P < 0.05$; Table 2.4). A significantly higher proportion of eels displaying a freshwater isotopic signature upon capture were classified in the Freshwater Residency Group in both years as a result of long-term activity in the vicinity of the antenna array or array detections during the Summer Period. Contrastingly, a significantly higher proportion of eels with a saline isotopic signature upon capture were classified in the Saline Residency, Spring-Summer Migration, and Summer-Fall Migration groups in 2009 and 2010 as a result of portable antenna identifications in the estuary and array detections within the migration periods.

The canonical discriminant analysis determined that δ^{13}C and δ^{15}N values were good predictors of whether an eel would display freshwater resident vs. amphidromous behaviours with highly significant discriminant functions generated for both years (P <0.001; Table 2.5). Mean discriminant function values by group indicated that classification to the amphidromous group (i.e., eels collectively classified in the Saline Residency, Spring-Summer Migration, and Summer-Fall Migration groups) corresponded to enriched ^{13}C and ^{15}N, whereas, classification to the freshwater resident group (i.e., eels classified in the Freshwater Residency group) corresponded to depleted ^{13}C and ^{15}N in both years (Figure 2.5). Correctly predicted group membership was 94% and 80% for amphidromous and freshwater resident grouped eels, respectively, in 2009 (Table 2.5). In 2010, correctly predicted group membership was 90% and 100% for amphidromous and freshwater resident grouped eels.

Correction factors for δ^{13}C and δ^{15}N

Storage of pectoral fin tissue in ethanol was found to significantly alter δ^{13}C and δ^{15}N values and a correction factor was required (Paired *t* test: δ^{13}C t = 17.76, df = 26, P <0.001; δ^{15}N t = 4.52, df = 26, P <0.001). Slopes of regressions relating δ^{13}C and δ^{15}N values from the two storage methods were not significantly different than a slope of 1 (*t* test: δ^{13}C t = 1.00, df = 25, P = 0.33; δ^{15}N t = 1.59, df = 27, P = 0.12). Therefore, constant correction factors of -1.83‰ and -0.28‰, representing the mean difference of analyzed values, were applied to δ^{13}C and δ^{15}N values of all samples stored in ethanol

(Table 2.6). In addition, significant differences in δ^{13}C and δ^{15}N values were found in all comparisons between caudal fin, pectoral fin, and muscle tissues (Paired *t* test: Caudal-Pectoral δ^{13}C t = 2.19, df = 15, P <0.05; Caudal-Pectoral δ^{15}N t = 3.15, df = 15, P <0.01; Caudal-Muscle δ^{13}C t = 3.20, df = 19, P <0.01; Caudal-Muscle δ^{15}N t = 19.32, df = 19, P <0.001; Pectoral-Muscle δ^{13}C t = 2.53, df = 15, P <0.05; Pectoral-Muscle δ^{15}N t = 14.62, df = 15, P<0.001). Regression slopes comparing δ^{13}C and δ^{15}N values of pectoral fin, caudal fin, and muscle tissue muscle were not significantly different than a slope of 1, with the exception of the caudal fin and muscle comparison for δ^{15}N (*t* test: Caudal-Muscle δ^{13}C t = 0.17, df = 18, P = 0.87; Caudal-Muscle δ^{15}N t = 2.79, df = , P <0.05; Pectoral-Muscle δ^{13}C t = 1.54, df = 14, P = 0.15; Pectoral-Muscle δ^{15}N t = 1.25, df = 14, P = 0.23). In addition, it was determined that caudal fin tissue requires a constant δ^{13}C correction factor of -0.72‰ and the following formula for δ^{15}N correction representing the slope of the regression: $\delta^{15}N_{Muscle} = 0.932*(\delta^{15}N_{Caudal}) - 0.606$. All isotope values described displayed in this study have had appropriate correction factors applied so that they represent pectoral fin tissue collected without the use of a preservative.

2.4.2. Seasonal Movements of Radio Transmitter Implanted Eels

Seasonal movements of radio-tagged eels in 2009 were consistent with patterns identified for PIT tagged eels (Figure 2.6). Of the nine eels radio-tagged in the spring of 2009 (#1-9), seven had a saline isotopic signature and two had a freshwater isotopic signature. Six of the seven eels with a saline isotopic signature migrated to saline habitat within the

Spring-Summer Migration Period and the first four days of the Summer Residency Period. The eel with a saline signature that remained in fresh water did so until battery death in December of 2010 (#1; Figure 2.6). The two eels with freshwater signatures remained in freshwater habitat until one eel was found deceased (#8) and the second eel remained in fresh water until battery death occurred in February of 2010 (#6; Figure 2.6). All habitat transitions during the Spring-Summer Migration Period were from freshwater to saline habitat.

Five eels (#10-14) were captured and radio-tagged in the estuary during the Summer Residency Period of 2009; all of which had a saline isotopic signature upon capture. These eels remained within the estuary or escaped detection range beyond the mouth of the river during the Summer Residency Period. Eels made long-distance movements while inhabiting the estuary in summer, frequently beyond the mouth of the river and outside the detection area. In contrast, eels inhabiting fresh water during the summer residency period exhibited relatively short-distance movements only (maximum distance moved 0.41 rkm by eel #6).

Three tagged eels moved from saline habitat to freshwater habitat during the Summer-Fall Migration Period including one eel tagged in spring (#5) and two eels tagged in the estuary in summer (#13 and 14). In addition, one eel tagged in spring (#4) returned from beyond the mouth of the river to approximately 1.18 rkm, 0.3 km downstream of the head of salinity. Eel #6 which exhibited a freshwater isotopic signature upon capture also undertook a long-distance upstream movement within fresh water during the Summer-

Fall Migration Period where it became the most upstream observed eel at 3.1 km. In contrast to the Spring-Summer Migration Period, all long-distance movements and interhabitat transitions during the Summer-Fall Migration Period were directed upstream. Eel #15 was captured 0.17 km upstream of the head of salinity in fresh water during the Summer-Fall Migration period and released at the location of capture. The eel was found to exhibit a freshwater isotopic signature and remained in fresh water following release (Figure 2.6).

No interhabitat or long-distance movements were exhibited during the Winter Residency Period by the initial 15 eels tagged prior to the onset of Winter Residency Period. However, 12 eels (#16 to 27) eels radio tagged in late October, 2009, following capture by electrofishing between 0.17 and 0.31 km upstream of the head of salinity made contrasting movements to those tagged previously. Of the 12 tagged eels, four remained in fresh water following release. All other eels transitioned outside the survey area, presumably beyond the mouth of the river, within 35 days of release, four of which were identified within the estuary prior to exiting the survey area. By December 15, 2009, no eels remained within the survey area, with the exception of eels #4 and 12 which resided together in the estuary near the head of tide in a deep pool in the area of pilings remnant of a former dam, and eel #19 which resided in an area dominated by boulder and cobble substrate 0.14 km downstream of the head of salinity.

Throughout the study period, eels in fresh water were exclusively found within the interstitial spaces of rocks and boulders which were the predominate substrates. Within

the estuary which is dominated by a sandy to gravely substrate with small amounts of silt, all radio transmitter implanted eels were located at least once within the interstitial spaces of uncommon substrates, including boulders or woody debris. Only three eels were located in areas with substrate typical of the estuary and were identified in these areas amongst cover provided by mats of green algae (*Ulva intestinalis*).

2.5. DISCUSSION

This study has shown that yellow-stage American eels in the Upper Salmon River undertake seasonal amphidromous migrations between saline summer foraging habitat and freshwater overwintering grounds, while other eels remain in fresh water throughout the foraging season. The migration evidence is sufficient to conclude the hypothesis of Clément et al. (In Prep.) that observed classes in δ^{13}C and δ^{15}N values for spring-captured eels are driven by variation in seasonal movements and associated habitat and not the immigration of saline prey items to freshwater habitat. Clément et al. (In Press) found that spring-captured eels in the Upper Salmon River displayed both saline isotopic and microchemical signatures with no evidence of freshwater habitat use, although the current study shows that this same group of eels are likely to have overwintered in fresh water following migration from saline habitat the previous year. The results provide further evidence that both stable isotopes and otolith records fail to detect overwintering habitat use due to reduced elemental turnover and growth rates, and slow otolith accretion at low temperatures (Thibault et al. 2007b). American eels in eastern Canada winter in substrate shelters where they exhibit little activity (Tomie et al. 2013). Both the

overwinter retention of the saline isotopic signature from the previous foraging season and the lack of detectable otolith accretion during winter can be contributed to winter quiescence (Walsh et al. 1983). Therefore, studies enumerating populations of yellow eels in saline habitats must not assume that sampled eels are strictly saline residents based on isotopic or microchemical signatures, as some eels may utilize freshwater habitat for overwintering and these periods can be undetected in isotopic and microchemical records.

It can also be concluded from this study that American eels appear to retain patterns in seasonal habitat use from year to year because eels were more likely to utilize habitats in the year of release characteristic of their isotopic signatures upon capture (i.e., freshwater vs. saline) which were reflective of habitat use in the previous year. Consistency in seasonal habitat use from the previous year was corroborated by significant cluster group and discriminant function analyses. These tests independently related δ^{13}C and δ^{15}N values, retained from the previous year, to observed behaviours following release. In addition, the identification of eels tagged in 2009 making directed movements in the spring of 2010 and residing in the estuary in the summer of 2010 further supports annual movement patterns.

Although this study identified consistency in habitat use by American eels between years, there were instances in which eels predicted to utilize saline or freshwater habitat based on stable isotopic signatures were observed doing the opposite using telemetry including radio-tagged eel #1. Some American eels have been shown to sporadically transition between saline or freshwater habitat use as identified through otolith microchemistry

(Thibault et al. 2007b; Jessop et al. 2008). Therefore, one could consider the percentage of misclassified PIT tagged eels in the discriminant function analysis, ranging from 6% to 20%, as a rough estimate of the proportion of eels switching seasonal habitat use patterns, between years. However, these values are likely overestimates of the percentage of eels switching tactics as many eels displaying a freshwater signature upon capture (i.e., FWS eels) were identified below the maximum high tide head of salinity but above the minimum high tide head of salinity using the portable antenna detector in summer. As a result, these specific eels were categorized in the amphidromous group of the discriminant analysis. Although these eels were below the maximum, or spring-tide head of salinity, the area in which they were located is subjected to complete freshwater habitat for much of the Summer Residency Period.

One radio-tagged eel (#6) displaying a freshwater isotopic signature upon capture was observed undertaking an upstream migration beginning and ending in fresh water during the Summer-Fall Migration Period. This suggests that seasonal migrations may not be restricted to eels undertaking habitat transitions between saline and freshwater habitats in the Upper Salmon River. That freshwater resident eels also undertake spring downstream and fall upstream migrations was also evidenced as 48 eels with freshwater isotopic signatures were captured in spring using methods that target downstream-migrating eels (i.e., RST and fyke nets). Activity in the vicinity of the antenna array was higher in the summer of 2009 than in 2010 when the array was moved approximately 200 m upstream of the 2009 location which suggests that some freshwater resident eels may be targeting

the area immediately upstream of the estuary for summer use. A blurred gradient in δ^{13}C and δ^{15}N values observed in spring-migrating eels, particularly in 2010, may be due to a combination of: foraging activities by some eels near the head of salinity in the previous year or year-to-year transitions between freshwater and saline foraging tactics. Such actions would result in a partial depletion or enrichment, respectively, of δ^{13}C and δ^{15}N to intermediate values.

It also appears that migrating eels utilized saline habitat during summer beyond the mouth of the river in addition to the estuary. Tracking of radio-tagged eels showed that most spring-tagged eels migrated downstream to the estuary and beyond the detection range, presumably outside the mouth of the river. In addition, radio-tagged eels made repeated appearances in the estuary throughout the Summer Residency Period which may represent long-distance foraging movements between the estuary and areas beyond the mouth of the river, at least by larger eels (>36 cm). Eels in saline habitat may undertake longer-distance movements compared to those in freshwater habitat by utilizing selective tidal-stream transport. Displaced estuarine American eels in Maine, USA, have exhibited selective tidal stream transport in relation to homing behaviour (Parker and McCleave 1997).

Habitat use by radio transmitter implanted eels in the estuary during summer differed from that characterized for PIT tagged eels which were almost exclusively identified within mats of green algae (*Ulva intestinalis*). Radio transmitter implanted eels were predominately identified in substrates containing larger interstitial spaces, including

boulders, wood pilings, and woody debris, all of which were relatively uncommon microhabitats in the estuary which primarily consisted of a sandy to gravely mixture interspersed with a small amount of silt. Eels in the estuary were most commonly identified in two locations during summer; near the head of salinity within pilings remnant of a former dam, and at the midpoint of the estuary, where the presence of a few boulders and woody debris provided some cover to larger eels. These differences were likely size-related. Eels implanted with radio transmitters in the spring and summer of 2009 had a mean size of 43.7 cm and a mean weight of 137.3 g. In contrast, PIT tagged eels had a mean size of 28.5 cm and a mean weight of 31.1 g. The cover utilized by small sized eels was probably insufficient to provide cover to large sized eels. An experimental study of Caribbean fish assemblages has shown that increasing the abundance of large shelters in a coral reef correlates proportionally to an increase in the abundance of large fish (Hixon and Beets, 1989). However, a corresponding increase in the abundance of small-sized fish was not observed.

Only two radio transmitter tagged eels were found to continuously overwinter in the estuary and both eels overwintered near the head of salinity within pilings and rip rap remnant of a former dam. Although technically within the estuary, and sometimes under saline influence, the pilings were within a relatively deep freshwater pool at low tide (>1.4 m) and, therefore, overwintering eels would remain under a high degree of freshwater influence. The boulders/pilings would also provide protection to eels from ice-scouring or predation. Eels which were found to overwinter elsewhere in the estuary

eventually disappeared from the detection area. All other overwintering sites were in fresh water where eels were found within the interstitial spaces of boulders, a prevalent substrate of the lower main stem of the Upper Salmon River.

It is unclear why radio-tagged eels captured in late October of 2009 undertook downstream movements following release to the estuary and beyond the mouth of the river, indicating that some eels may be undertaking alternative tactics of seasonal movement. Although these movements may have been natural, evidence suggests that the movements may have been anomalous. Most of the captured eels had saline isotopic signatures indicating that they probably foraged in the estuary in summer and exhibited upstream movement into fresh water prior to capture. This was also the only instance in which radio-tagged eels with freshwater isotopic signatures were observed undertaking interhabitat transitions to saline habitat and a corresponding migration of eels tagged previous to this event was not observed indicating that the movements may be anomalous. In addition, a corresponding directed movement of PIT tagged eels was not observed in late October following the radio tagging event. While all other eels were tagged using passive techniques (i.e., RST and fyke nets), these eels were captured via electrofishing which has been shown to be particularly harmful to American eels, likely due to their elongated form and, correspondingly, high vertebral count (Reynolds and Holliman, 2004). Electrofishing and disturbance of eels having already completed seasonal migrations to overwintering habitat may have elicited anomalous behaviour.

It has been suggested by Jessop et al. (2008) that seasonal migration from productive marine and brackish habitats to fresh water may be driven by the relative availability of suitable overwintering habitat, and that is likely the case in the Upper Salmon River. Estuarine American eels are known to overwinter in Canada by burrowing in mud, as determined by field observations of burrows and the presence of commercial and recreational eel spear fisheries in ice-covered and mud-bottomed bays and estuaries (Cairns et al. 2012). This may be a tactic used by eels to cope with sub-zero winter temperatures in saline waters by obtaining geothermal heat as American eels do not appear to possess blood antifreeze proteins (Tomie 2011) which allow some fish species to survive at subzero temperatures. The substrate of the Upper Salmon River does not appear ideal for burrowing as sediments range from a sandy to gravely mixture interspersed with a small amount of silt. Burrowing in such substrates is possible but takes much more time and energy than burrowing in mud or boulder crevices (Tomie et al. 2013).

A few days of intense cold in tidal estuaries of the Bay of Fundy can cause ice formations to the extent that the estuaries have been termed “ice factories” (Desplanque and Mossman 1998). The ice sheets produced by these “ice factories” move back and forth until settling in the estuary at low tide and this action can promote vigorous erosion (Desplanque and Mossman 1998). Scouring or ploughing of substrates by ice sheets may disrupt potential habitat for winter burrowing eels. Disrupted eels may not possess sufficient energy to search for more appropriate habitat due to reduced feeding in winter

or eels may be subjected to water temperatures low enough to freeze blood. Eels commonly overwinter while burrowed in substrate in estuaries of the Southern Gulf of St. Lawrence, Canada (Cairns et al. 2012; Tomie et al. 2013). Such estuaries encounter smaller tidal currents and water level fluctuations than those of the Bay of Fundy and the risk of disruption due to ice scouring is greatly reduced in comparison.

This study has shown that eels undertake seasonal amphidromous migrations in the Upper Salmon River. The results of this study has implications with respect to management of American eels. Morrison and Secor (2003) suggested that management regimes for the American eel should be developed specific to salinity zones due to growth and productivity differences between habitats. However, freshwater habitat use for overwintering by eels otherwise believed to be saline residents complicates such a management approach. This study highlights the need for unimpeded access between freshwater and saline habitats by yellow-stage eels even when otolith microchemistry implies a year-round occupancy of saline waters. Rivers and estuaries draining into the Bay of Fundy have a wide range of existing barriers to fish migration including dykes, aboiteaus, causeways, dams, and wharves (Wells 1999). The Upper Salmon River presents no exception and was once subject to significant timber harvesting and log driving and a dam was constructed at the upstream extent of the estuary which would have restricted habitat transitions of diadromous fish prior to its collapse in 1954 (Parks Canada 1997). Although the Upper Salmon River now offers unimpeded access between saline and freshwater habitats, many other systems of the Bay of Fundy still contain

barriers to fish migration. The geographic extent and proportion of eel populations inhabiting saline waters which undertake seasonal amphidromous migrations to fresh water for overwintering remains unknown and should be a focus of future studies.

2.6. ACKNOWLEDGEMENTS

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Table 2.1. Biological characteristics of radio transmitter implanted American eels captured in the Upper Salmon River in 2009.

Sample Collection					Total Length (cm)		Weight (g)	
Period	Location	Method	Tag Type*	n	Mean ± S.E.	Range	Mean ± S.E.	Range
22-May to 22-Jun	Fresh Water (1.7 rkm)	RST, Fyke Net	NTC-6-1	9	43.4 + 2.2	36.1-58.2	137.3 + 35.5	70.1-410.0
21-Jul to 10-Aug	Estuary (0.6 rkm)	Fyke Net	NTC-6-1	5	44.4 + 3.1	36.4-52.8	168.6 + 38.8	87.1-300.0
5-Oct	Fresh Water (1.5 rkm)	Fyke Net	NTC-3-2	1	31.2	-	47.3	-
22-Oct to 23-Oct	Fresh Water (1.5 to 1.8 rkm)	Electrofishing	NTC-3-2 (n=11), NTC-6-1 (n=1)	12	34.4 + 2.4	29.0-56.1	56.6 + 8.7	33.4-144.0

* Radio transmitters were coded-wire nanotags by Lotek Wireless. NTC-6-1 tags weighed 2.8 g in air and had an estimated battery life of 232 days whereas NTC-3-2 tags weighed 1.1 g in air with estimated battery life of 124 days. RST = rotary screw trap. N.B. The maximum head of salinity was at approximately 1.5 rkm.

Table 2.2. Methods for classifying telemetric movements of PIT tagged yellow eels into behavioural groups.

*Rule #	Classification Rule	Behavioural Group
1	Portable antenna detection in the estuary during the Summer Residency Period in the year of release.	Spring-Summer Migration & Saline Residency
2	Fixed antenna array detection on ≥4 evenings in the year of release.	Freshwater Residency
3	Fixed antenna array detection during the Summer Residency Period.	Freshwater Residency
4	Fixed antenna array detection during the Spring-Summer Migration Period following release.	Spring-Summer Migration
5	Fixed antenna array detection during the Summer-Fall Migration Period.	Summer-Fall Migration
n/a	No telemetric data in the year following release.	Unclassified

*Rules numbered in order of confidence for classifying a particular movement based on the method used. Eels classified using rule #1 were exempted from classification as freshwater residents using rules #2 or #3. Eels classified in the Freshwater Residency group were exempted from classification using rules #4 or #5.

Table 2.3. Physical and isotopic parameters of PIT and radio-tagged American eels captured in the Upper Salmon River, New Brunswick, Canada, in 2009 and 2010 including statistics for cluster-grouped eels in each year.

Year	Cluster Group	n	Length (cm)			Weight (g)			$\delta^{13}C$			$\delta^{15}N$		
			Mean	CI	SD	Mean	CI	SD	Mean	CI	SD	Mean	CI	SD
2009	Total	163	29.3	0.7	4.4	37.0	5.4	35.2	-13.9	0.6	4.0	12.2^{A}	0.3	1.7
	SAS	140	29.4	0.7	4.5	37.5	6.2	37.4	-12.5	0.3	2.1	12.8	0.1	0.8
	FWS	23	29.0	1.7	4.3	33.7	6.7	16.4	-22.3	0.8	2.0	8.6	0.3	0.8
2010	Total	134	28.9	0.7	4.1	32.8	4.0	23.7	-14.6	0.7	3.9	11.7^{B}	0.3	1.6
	SAS	109	28.8	0.8	4.2	32.3	4.7	25.3	-13.0	0.4	2.2	12.3	0.2	0.9
	FWS	25	29.3	1.3	3.3	35.1	5.5	14.2	-21.7	0.5	1.2	9.1	0.4	1.1

NB SAS = Saline Signature, FWS = Freshwater Signature, CI = 95% Confidence Interval, SD = One Standard Deviation. Different letters indicate significant difference in cluster group means within a given year or significant difference in between-year comparisons of total values (t-test, $P < 0.05$).

Table 2.4. Comparisons of the proportion of SAS and FWS eels and passive integrated transponder (PIT) telemetry-classified behavioural groupings for the year of release.

	Isotopic Signature Grouping Upon Capture			
	2009		2010	
PIT Telemetry-Classified Behavioural Group	SAS (n=133)	FWS (n=21)	SAS (n=110)	FWS (n=24)
Freshwater Residency Group	2 %[a]	38 %[b]	0 %[a]	24 %[b]
Saline Residency Group	41 %[a]	0 %[b]	39 %[a]	13 %[b]
Spring Migration Group	55 %[a]	24 %[b]	78 %[a]	33 %[b]
Fall Migration Group	56 %[a]	5 %[b]	n/a	n/a

NB SAS = Saline Signature, FWS = Freshwater Signature. Different letters indicate significant difference in proportion of isotope-grouped eels categorized in a specific behavioural group in a given year (Fisher's Exact Test, $P < 0.05$).

Table 2.5. Results of canonical discriminant function analysis on two foraging groups (i.e., Amphidromous and Freshwater (FW) Resident American eels) as determined using PIT telemetry in the Upper Salmon River, New Brunswick, Canada.

		2009 Function 1	2010 Function 1
Eigenvalue		0.534	0.373
Canonical correlation		0.590	0.521
F		28.32	17.91
df 1		2	2
df 2		106	96
P		<0.0001	<0.0001
Standardized canonical discriminant function coefficients			
$\delta^{13}C$		0.037	0.436
$\delta^{15}N$		0.972	0.646
Classification results			
Year	Actual group	Predicted group membership (percent)	
		Amphidromous	FW Resident
2009	Amphidromous	93 (93.9)	6 (6.1)
	FW Resident	2 (20.0)	8 (80.0)
2010	Amphidromous	85 (90.4)	9 (9.6)
	FW Resident	0 (0.0)	5 (100.0)

Table 2.6. Between-tissue and between-storage correction factors for $\delta^{13}C$ and $\delta^{15}N$ values derived from stable isotope analysis

	Difference Significant?	Correction Factor	
		$\delta^{13}C$	$\delta^{15}N$
Pectoral Fin Preservation in Ethanol			
Ethanol Preserved → Frozen/Dried Tissue	Yes	-1.83‰	-0.28‰
Fin Tissue vs. Fin Tissue			
Pectoral Fin Tissue → Caudal Fin Tissue	Yes	0.36‰	0.20‰
Fin Tissue vs. Muscle Tissue			
Pectoral Fin Tissue → Muscle Tissue	Yes	-0.58‰	-1.13‰
Caudal Fin Tissue → Muscle Tissue	Yes	-0.72‰	$0.932*(\delta^{15}N_{Caudal}) - 0.606$

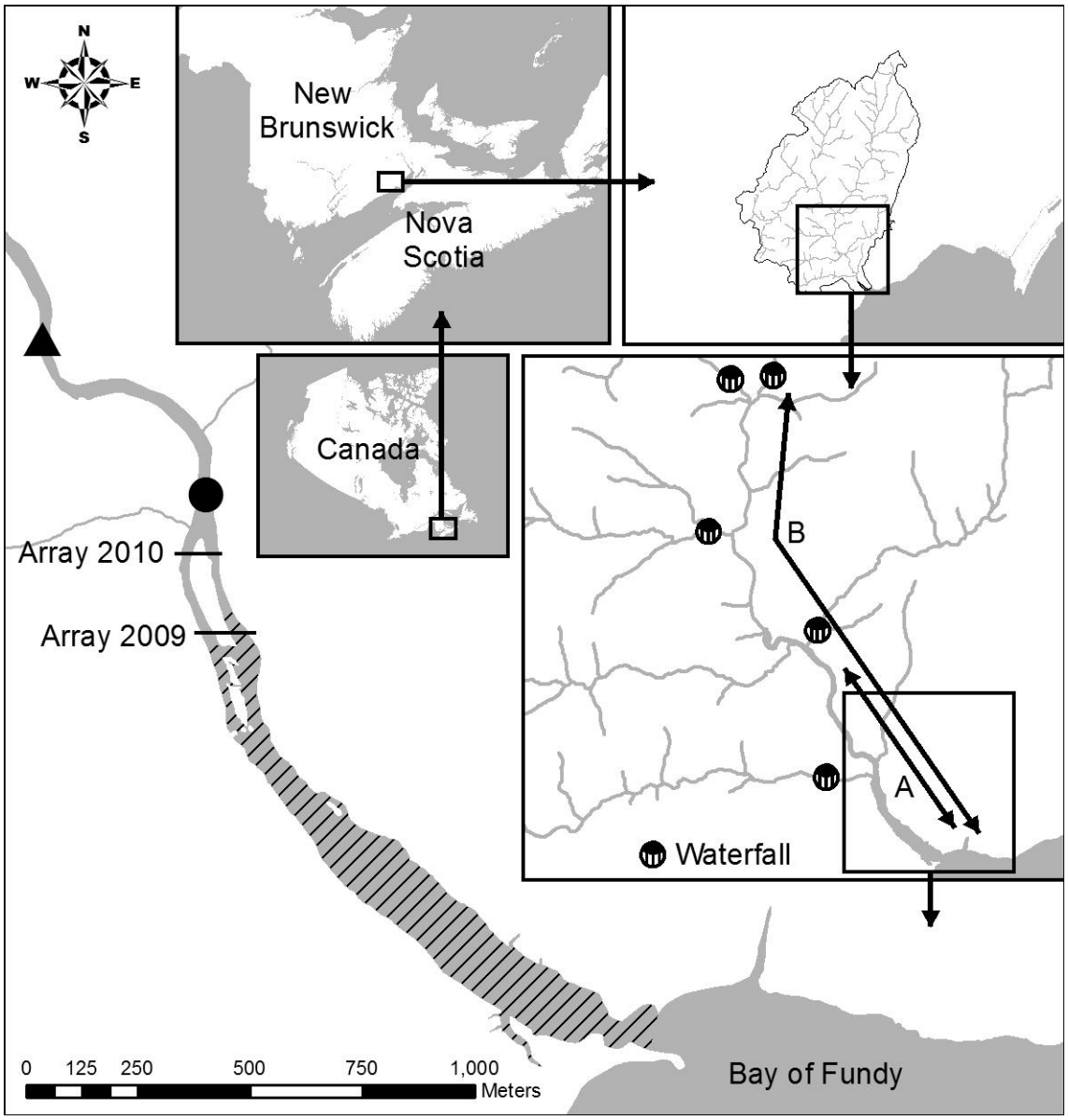


Figure 2.1. Map of the Upper Salmon River in New Brunswick, Canada. The capture location (black circle), the release location (black triangle), and the locations of the PIT antenna array in 2009 and 2010 are shown. The hatched area of the river represents the estuary or saline-influenced area of the river. Lineal area of the river's main stem manually radio tracked during regular (A) and complete (B) tracking events are shown.

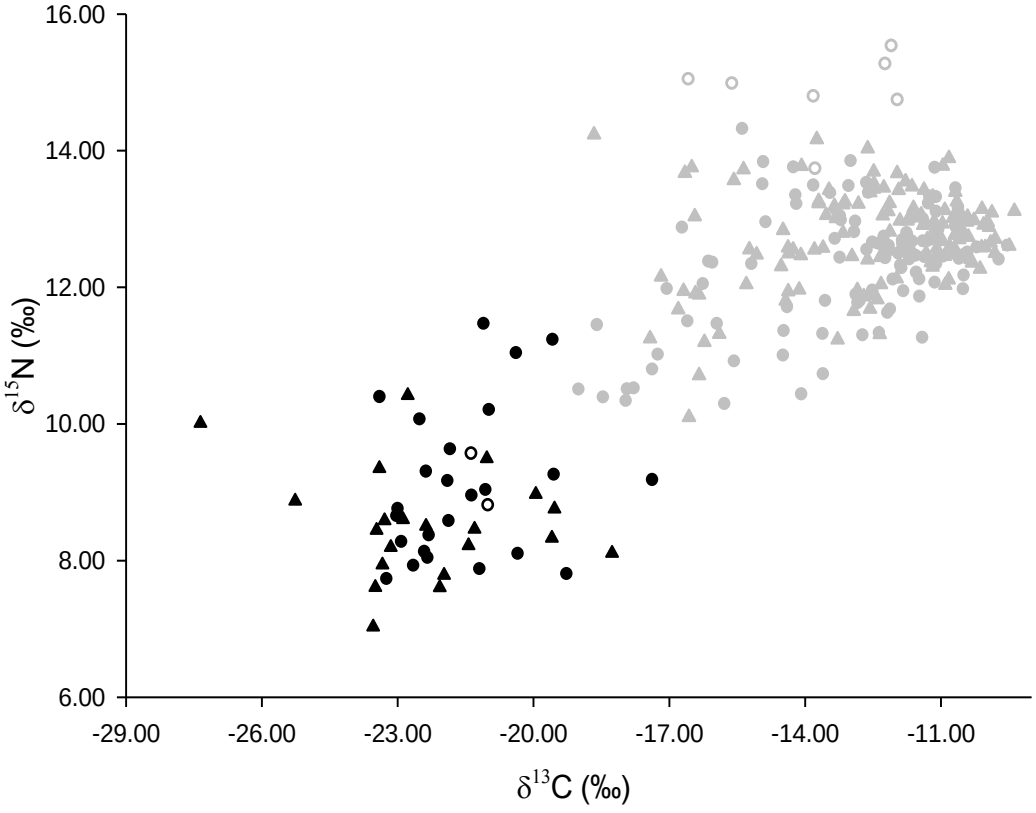


Figure 2.2. Scatterplot of δ^{13}C and δ^{15}N values (‰) of PIT tagged (filled symbols) and radio-tagged (empty symbols) American eels captured in the spring of 2009 (circles) and 2010 (triangles). The two cluster groupings are distinguished by black symbols (Freshwater Signature; FWS) and gray symbols (Saline Signature; SAS).

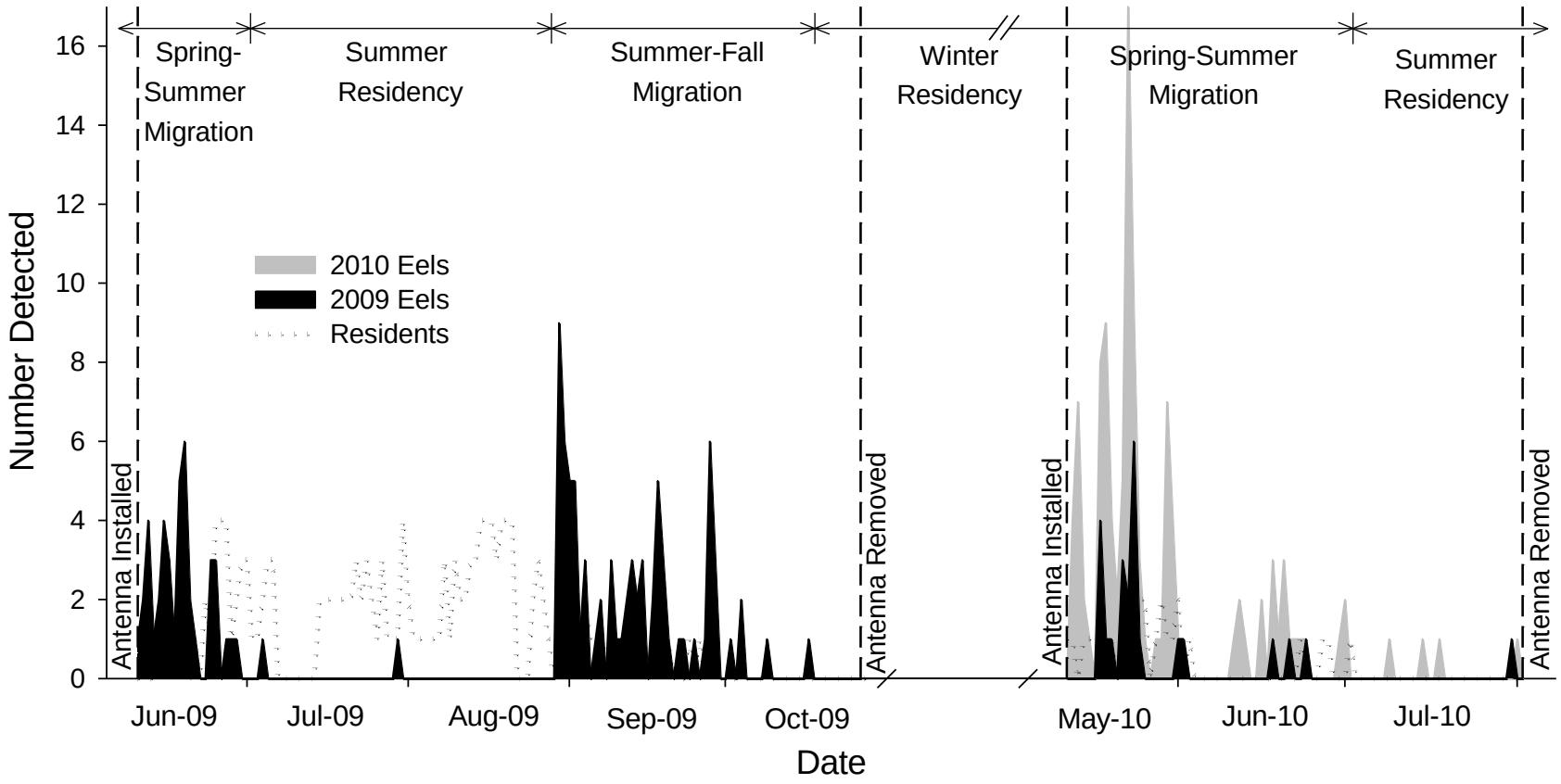


Figure 2.3. Summary of American eel movements as detected by the PIT antenna array. Peaks represent the total number of unique individuals, tagged in 2009 (black shaded area; n=97) and 2010 (grey shaded area; n=99), that were detected by the antenna array on a given night. To distinguish between periods of directed movement and resident eel activity, those individuals detected at the antenna array over repeated nights were graphed separately as residents (dotted line; n=16). Movement periods were identified based on changes to observed activity rates and are indicated at the top of the graph.

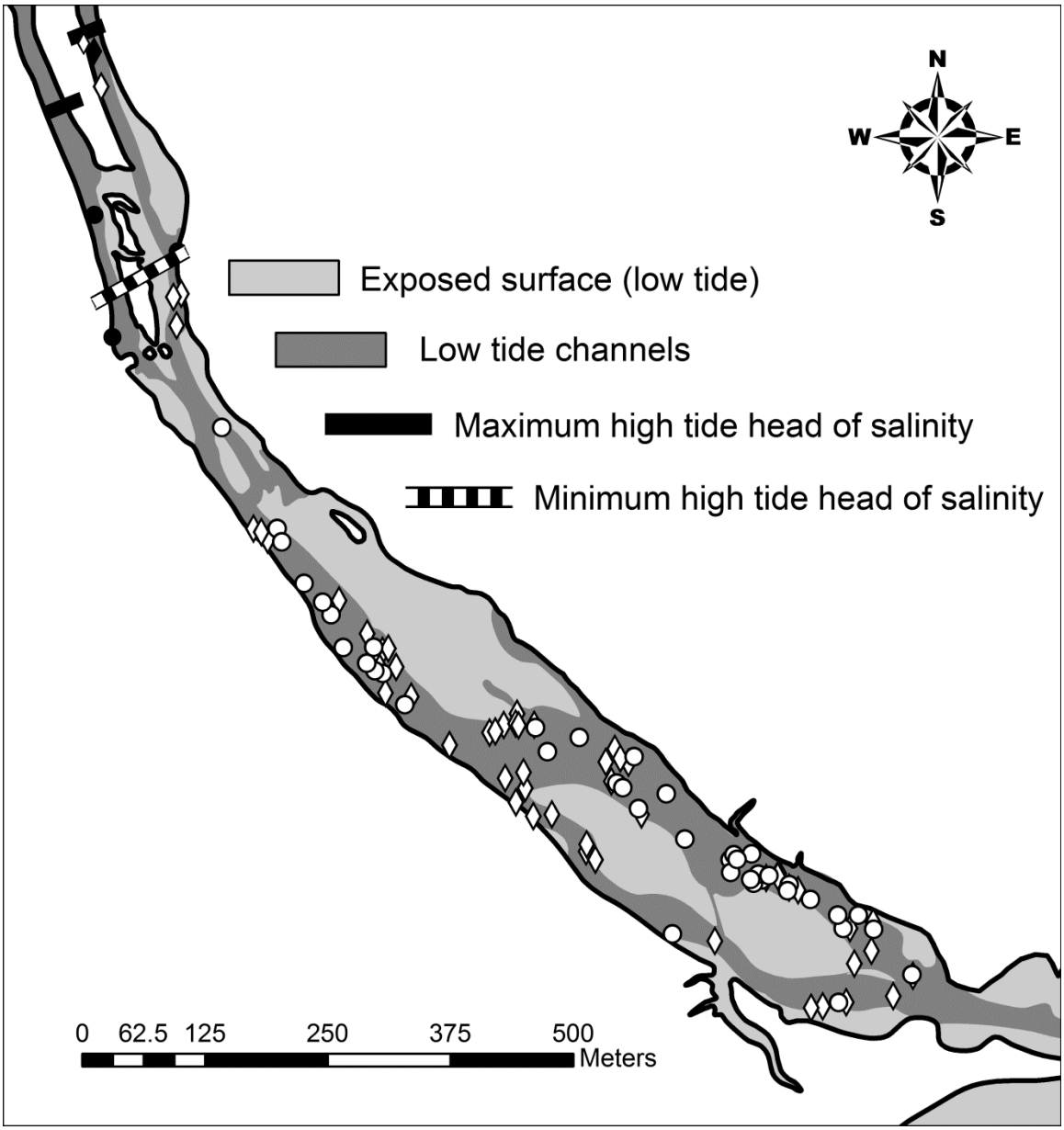


Figure 2.4. Results of portable antenna sweeps in the Upper Salmon River estuary during the Summer Residency Periods of 2009 and 2010. The illustrated portion of the river defines the area surveyed in each year. Symbols indicate the location of 2009 (diamonds) and 2010 (circles) PIT tagged American eels in the summer of release. Cluster-group membership for freshwater (FWS) and saline (SAS) signature groups is indicated by filled and empty symbols, respectively. For clarity, the locations of 2009-tagged American eels in 2010 are not shown but followed a similar pattern with respect to habitat utilization.

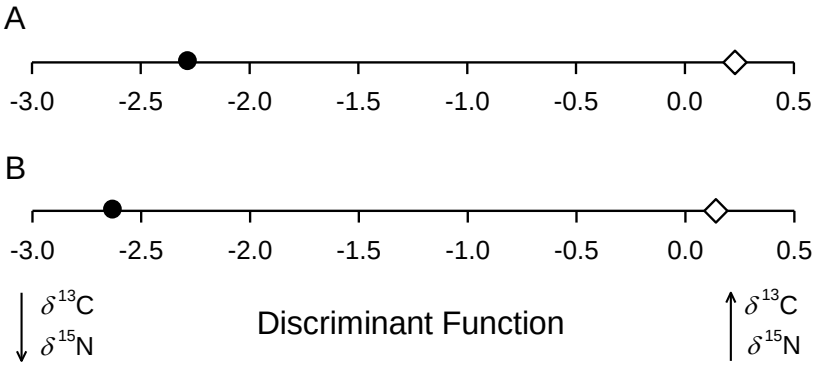
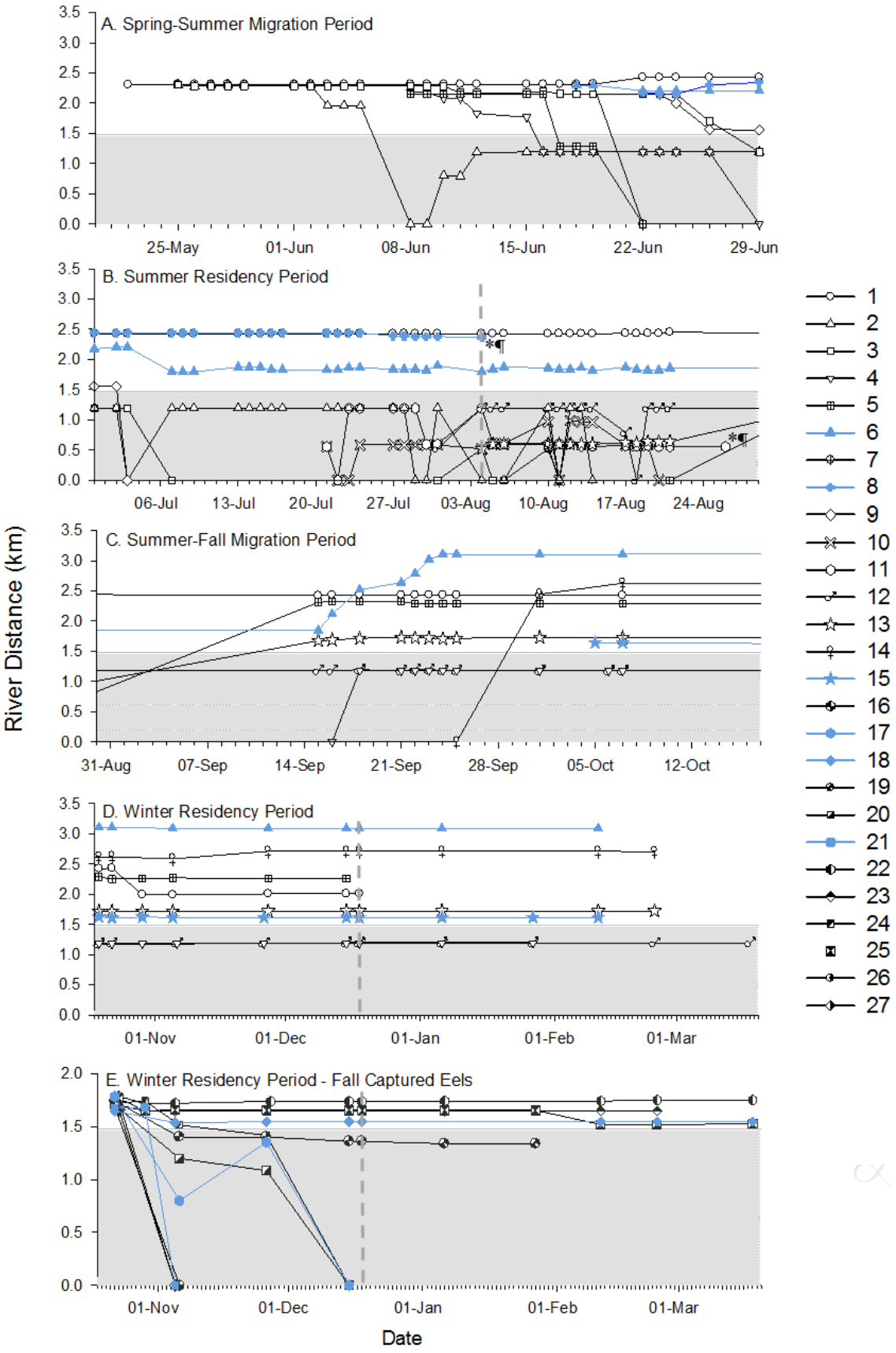


Figure 2.5. Results of canonical discriminant function analysis relating δ^{13}C and δ^{15}N isotopic values to observed behaviours as determined using telemetric data in a) 2009 and b) 2010. Symbols represent the mean discriminant function values for American eels exhibiting freshwater resident (empty diamonds) and amphidromous (filled circles) behaviours. As indicated, the discriminant function is positively correlated with both δ^{13}C and δ^{15}N values.

Figure 2.6. Seasonal movements of individual radio transmitter implanted American eels during the Spring-Summer Migration Period (A), Summer Residency Period (B), Summer-Fall Migration Period (C), and Winter Residency Period of 2009/2010 (D). Movements of radio-tagged eels captured in the fall or 2009 are graphed separately for clarity (E). Individual eels are denoted by a unique symbol. Blue, filled symbols represent eels with a freshwater isotopic signature upon capture and all other symbols represent eels with a saline isotopic signature. The initial appearance of symbols denotes the date and location (i.e., river distance) of release following tagging and the final symbols indicate the last known location prior to battery death. Where the final location is denoted by an asterisk (*), the eel was found dead or sacrificed intentionally following recapture. Lines drawn between symbols and the x-axis are inferred movements based on absence of detection during a tracking event. The shaded area represents saline habitat (i.e., the estuary). Vertical dashed lines indicate the dates of complete-river radio tracking events (0 - 8.6 rkm).


A. Spring-Summer Migration Period
B. Summer Residency Period
C. Summer-Fall Migration Period
D. Winter Residency Period
E. Winter Residency Period - Fall Captured Eels
River Distance (km)
Date
25-May
01-Jun
08-Jun
15-Jun
22-Jun
29-Jun
06-Jul
13-Jul
20-Jul
27-Jul
03-Aug
10-Aug
17-Aug
24-Aug
31-Aug
07-Sep
14-Sep
21-Sep
28-Sep
05-Oct
12-Oct
01-Nov
01-Dec
01-Jan
01-Feb
01-Mar
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3. Environmental correlates of amphidromous migration by yellow-stage American eels (*Anguilla rostrata*) in the Upper Salmon River, New Brunswick, Canada

3.1. ABSTRACT

A detailed examination of how migration timing of yellow-stage American eels *Anguilla rostrata*, correlates with seasonal and diel changes in environmental variables was completed in the Upper Salmon River, New Brunswick, Canada. The migrations of interest were seasonal amphidromous migrations between saline summer foraging habitats and freshwater overwintering habitat. Count regression models were used to examine how environmental variables correlated with spring downstream and fall upstream migration, as measured by total daily capture in a rotary screw trap in spring, or detection of passive integrated transponder (PIT) tagged eels at a fixed antenna array in fall. Water temperature and photoperiod were the best correlates of spring downstream migration with increased migration occurring throughout the run at higher temperatures and earlier in the run when photoperiod was shorter. Water temperature, river discharge, and lunar period were the best correlates of fall upstream migration with increased migration occurring throughout the run at lower temperatures, higher discharge, and at new and full moons. Circular statistics revealed a strong diel pattern with almost all migrations occurring during periods of darkness and centered about the midpoint of the

dark period. A weak but statistically significant tidal effect was found in spring-migrating eels in 2009 and 2010, with peaks occurring 3.7 h and 6.3 h following high tide in the two years, respectively. However, fall upstream migration was found to be random with respect to tide.

3.2. INTRODUCTION

Worldwide abundance of *Anguilla* eels is on the decline (Dekker *et al*., 2004). This includes the American eel, *Anguilla rostrata*, population which exhibited precipitous declines in the upper St. Lawrence River and Lake Ontario, Canada in the 1980s and 1990s (Castonguay *et al*., 1994; Casselman *et al*., 1997). These declines have highlighted the need for basic information on life-history parameters to aid managers in making decisions relating to fishing regulations, passage mitigation, and habitat alteration (Haro *et al*., 2000). The yellow or growth stage is the longest stage of the American eel life cycle (COSEWIC, 2012). Consequently, yellow eels are susceptible to anthropogenic impacts over the longest time period. The yellow eel stage is also the life cycle period that is spent in rivers and estuaries; areas which encounter higher anthropogenic impacts.

A recent study has shown that some yellow-stage American eels in the Upper Salmon River, New Brunswick, Canada, migrate seasonally between freshwater overwintering habitat and saline summer foraging habitat (Sweezey et al. Chapter 2). This movement pattern can be considered a seasonally amphidromous migration, defined as a diadromous form of migration (i.e., between salt water and fresh water) irrespective of life-cycle or

reproductive purposes (Myers, 1949). Amphidromous migrations of this nature have been reported for American eels through interviews with fisherman in Nova Scotia, Canada (Medcof, 1969) and through studies which have documented migrating yellow-stage eels (Smith and Saunders, 1955; Jessop, 1987; Thibault *et al*., 2007). Amphidromous migrations may be a tactic enabling eels at temperate or higher latitudes to forage in summer in productive saline habitat which is unsuitable for overwintering (Daverat *et al*., 2006; Jessop *et al*., 2008). Poor overwintering conditions in saline habitat may drive movements to freshwater overwintering habitat where overwintering eels may encounter stable substrates, enhanced cover, reduced predation, and lower environmental stress including suprazero temperatures (Edeline, 2007; Thibault *et al*., 2007; Jessop *et al*., 2008). The geographic extent over which migrations of this nature occur is unknown, however, monitoring programs using rotary screw traps (RST) in fast-flowing rivers have demonstrated the commonality of spring downstream "runs" of American eels in many eastern Canadian systems (Caron and Gauthier, 2003; Chaput and Jones, 2004; Clément *et al*., 2007; Cairns *et al*., 2007) and seasonal movements of this nature by the closely related European eel (*Anguilla anguilla*) have been commonly observed by fishers (Feunteun *et al*., 2003; Tesch, 2003).

Few studies have examined how environmental variables correlate with American eel movement. Jessop (2003) examined how the arrival of sea-origin migrating elvers in the East River, Nova Scotia, correlated over a ten year period with local atmospheric temperature (degree days above 11°C), mean June water temperatures, and local

precipitation as a measure of river discharge. However, no significant correlations were identified (Jessop 2003). Temperature has been found to be a positive correlate of yellow eel movement for the closely related European eel (*Anguilla anguilla*) in Norway (Vøllestad, 1986) and France (Baisez, 2001). Temperature, water level, and atmospheric pressure, in decreasing order of importance, were found to correlate significantly with catch per unit effort for two species of anguillid yellow eels, long-finned (*Anguilla reinhardtii*) and short-finned (*A. australis*) eels, in New Zealand (Jellyman, 1991). The lunar cycle has also been shown to correlate with the behaviour and movements of yellow-stage anguillid eels (Jellyman, 1991; Baras *et al*., 1998; Cairns and Hooley, 2003, Feunteun *et al*., 2003). Cairns and Hooley (2003) reviewed relations between anguillid eel activity and lunar cycles and found that distinct lunar cycles were commonly observed, but the timing of the peaks varied widely with life history stage and geographic location.

In addition to seasonal changes in environmental factors associating with yellow eel movement, eel behaviour has been shown to correlate with daily fluctuations in diel and tidal cycles (Parker, 1995; Baras *et al*., 1998; Baisez, 2001). Yellow-stage American eels have been shown to be nocturnal and exhibit greater movement in nighttime periods as shown through acoustic and ultrasonic telemetry (Thibault *et al*., 2007, Helfman *et al*., 1983). Similar observations have been made for other species including the European eel (Baras *et al*., 1998, Baisez, 2001) and for long-finned and short-finned eels in New Zealand (Jellyman and Sykes, 2003).

This study examines the timing of seasonal amphidromous migrations of yellow-stage American eels in the Upper Salmon River to identify environmental correlates of migration; a first step in elucidating the influence of environmental changes on amphidromous eel migration. We examined detailed migratory profiles in 2009 and 2010 derived from daily trends in fish capture by a rotary screw trap, and trends in Passive Integrated Transponder (PIT) tagged eel migration as measured using a fixed-location PIT antenna array.

3.3. METHODS

3.3.1. Study Area

The Upper Salmon River (45º36'N, 64º56'W) has a drainage area of 177 km^2 and is located in south-eastern New Brunswick, Canada, where, in the lower reaches, it borders Fundy National Park (Figure 3.1). In the lowest 9 km of the system, the main stem is typically comprised of fast-flowing riffle and run habitat and substrate is dominated by coarse substrates; primarily boulders. The lowest 1.5 km of the river, from the mouth to the limit of salt penetration (i.e., head of salinity), comprises the estuary. The estuary is subjected to extreme semi-diurnal tidal fluctuations characteristic of the inner Bay of Fundy. At low tide, the estuary consists of shallow freshwater channels bordered by tidal flats. With the incoming tide, the estuary slowly floods with waters upwards of 29 ppt in salinity until the surface area of estuarine water doubles in size. In contrast to the river's main stem, the estuary substrate in the estuary consists primarily of a sandy to gravely mixture covered in a fine layer of silt.

3.3.2. Data Collection

Yellow-stage American eels were captured while migrating downstream in the spring of 2009 and 2010 using a rotary screw trap (RST) and two fyke nets directed to target downstream-moving fish. Fishing gear were installed 200-250 m upstream of the maximum head of salinity (Figure 3.1). Captured eels were anaesthetized in a 250 ppm solution of tricaine methanesulphonate (MS-222; Argent Laboratories, Redmond VA) and water until a state of immobility was observed, then weighed, measured, and those eels that were larger than 25 cm in total length were implanted with 23 mm glass-encapsulated passive integrated transponder (PIT) tags [Texas Instruments (TIRIS^{TM}) model RI-TRP-RRHP, 134.2 kHz]. PIT tags were surgically implanted into the abdominal cavity following the methods of Roussel *et al*., (2000). The incision area was sealed using a single drop of n-butyl cyanoacrylate (Vetbond^{TM} surgical glue) to reduce tag loss and promote healing. Ten day control holds were completed for 20% and 17% of American eels tagged in 2009 and 2010, respectively, and tag retention was determined to be 100% with no adverse effects relating to tagging identified. However, four eels were immediately euthanized during tagging due to surgical complications. All other captured eels were released on the day of tagging, and no more than two days following capture. Eels captured one to two days prior to the day of tagging were held in live boxes in the same manner as control-holds. All procedures were carried out according to the Canadian Council on Animal Care guidelines and were approved by the Animal Care Committee of both the University of New Brunswick (Protocol #09043/10003) and Fisheries and Oceans Canada Maritimes Region (Protocol #09-11). In total, 154 and 134

American eels were PIT tagged in the springs of 2009 and 2010, respectively, after which they were released approximately 600 m upstream of the capture location (i.e., 2.3 rkm; Figure 3.1).

A flatbed PIT antenna array and system (Technologie Aquartis), was installed near the head of salinity to monitor transitions between freshwater and estuarine habitats in spring and fall (Figure 3.1). The antenna array consisted of four elongated rectangular antennae (1 m x ~15 m) placed end to end so that the entire width of the river was monitored for fish passage, and was secured to the substrate using rebar and large rocks. The antenna array was installed during the early stages of the downstream eel migration, or run, in both years and operated between May 17 and October 17 in 2009 and between May 14 and August 2 in 2010. Therefore, fall upstream migrations of yellow eels were examined in 2009 only. The antenna array was moved 200 m upstream of its 2009 location in 2010 (Figure 3.1) as it was found in 2009 to be under saline water influence during spring tide events and saline water attenuates radio signals. When a tagged eel was detected at the antenna array, the identification of the tagged eel and the associated time of detection were recorded by the system for later retrieval.

Mean daily water temperature (ºC) was collected using temperature dataloggers (VEMCO Minilog©) installed next to the fyke nets in fresh water. Water temperature values in the first two weeks following RST installation in 2009 were predicted using a temperature datalogger installed near the mouth of a brook adjacent to the capture area (Kinnie Brook; 80 m downstream). A linear regression with independent variables:

Kinnie Brook temperature, discharge (i.e., in the Upper Salmon River), photoperiod, minimum, maximum, and average atmospheric temperature, and precipitation, was completed to describe known average daily river temperature values ($R^2 = 0.86$, n = 115, $p < 0.0001$) and then missing values were predicted using the resulting regression equation. Mean daily discharge (m^3/s) was measured in the Point Wolfe River (7 km SW of the study site) and converted to discharge values for the Upper Salmon River which were found in a Parks Canada study over a period of three years (1976-1978) to be linearly correlated; with the Upper Salmon River discharge rate 1.22 times greater than the Point Wolfe River (Matthew Smith, GIS Specialist, Fundy National Park of Canada, personal communication). Discharge values from the Point Wolfe River, provided by Environment Canada, were collected using a pressure-actuated bubbler gauge transmitter (Hydrologic Alphe 3030, Grenoble, France) coupled to a data logger/transmitter (Sutron 8210, Sterling, VA, USA). Average daily atmospheric pressure (kPa) and atmospheric temperature values (ºC) were obtained from the Environment Canada National Climate Data and Information Archive for the Fundy National Park station. Photoperiod (h) was calculated as the time between sunrise and sunset obtained from the National Research Council of Canada for the nearest listed city (Moncton, NB). Time and date of high tide events were obtained from the Canadian Hydrographic Service (CHS) for Herring Cove, New Brunswick, which is situated within 3 km of the Upper Salmon River.

3.3.3. Data Analysis

We used count regression models to examine the relationship between amphidromous migration and environmental parameters. Global models included eight environmental parameters as independent variables: mean daily water temperature (ºC), mean daily discharge (m^3/s), average daily atmospheric pressure (kPa), photoperiod (h) and four variables for lunar period. The lunar period was treated as a circular or cyclical distribution (Batschelet 1981) and four variables were used to examine associations between lunar periodicity and migration through periodic regression using the equation of deBruyn and Meeuwig (2001):

$$\beta_5 \sin \sigma_i + \beta_6 \cos \sigma_i + \beta_7 \sin 2\sigma_i + \beta_8 \cos 2\sigma_i,$$

where σ is the angular transformed day of the lunar cycle (day/30 X 2π). The first two terms were included to determine if a single peak in migration occurred within the lunar cycle [Lunar (1p)], whereas the additional two terms were included to determine if a semilunar cycle, in which two peaks in migration occur per lunar cycle [Lunar (2p)], occurred (deBruyn and Meeuwig, 2001). Independent variables were examined for collinearity during model development because collinearity can have spurious effects on regression diagnostics, including interpretation of coefficient significance and direction of effect (Besley *et al*., 1980). Collinearity was tested using a linear regression for the global models and subsequent calculation of tolerance statistics. The tolerance statistic is equal to $1-R^2_x$ where R^2_x is the variance in each independent variable (x) explained by all other independent variables and tolerance statistics of <0.2 indicate "cause for concern"

whereas values <0.1 indicate a "serious collinearity problem" (Menard, 2001). The results for the downstream migration model indicated that collinearity was not an issue, as all values were ≥0.26. However, the upstream migration model indicated a potential collinearity issue for photoperiod and temperature due to the low observed tolerances statistics of 0.15 and 0.16, respectively. All other variables had values ≥0.77. Therefore, models containing both photoperiod and temperature for the fall upstream migration must be interpreted with caution.

For the spring downstream migration, we used the total daily capture (i.e., number of eels) by the RST in 2009 and 2010 as the dependent variable in count models because this represented the most complete characterization of the downstream "run" in both years. Data from 18 days in 2009 and 15 days in 2010 were discarded because the RST was raised, jammed, or not turning due to very low discharge rates. All other data between installation and removal in 2009 and 2010 were included in the count models. For the fall upstream migration, the number of PIT tagged eels detected migrating upstream per night, within the fall migration period, was used as the dependent variable in the count regression models. Eels were classified as migrating upstream if they were detected by the antenna array during a period of directed movement observed between August 18 and October 26, 2009 with the exception of those eels determined to be freshwater residents through tracking activities in a complementary study (Sweezey et al. Thesis Chapter 2). This event was considered directed upstream movement as 80% (43/54) of eels identified at known locations in the estuary in the summer of 2009, were

detected while undertaking directed movement during this period. We developed global models which treated all 8 independent variables and examined both Poisson and negative binomial regression models. Using the likelihood ratio test, overdispersion was detected for both downstream (G^2 = 277.17, P <0.0001) and upstream (G^2 = 8.67, P <0.01) migration Poisson models and, therefore, the negative binomial regression model was preferred in both cases. The Vuong test was used to determine if zero-inflated negative binomial models were preferable as they tend to be better at predicting excess zeros, which are common in studies of this nature (Long and Freese, 2006). Photoperiod was used as the inflate portion of zero-inflated models as it is a likely factor in predicting times of year when no migration occurs (McCormick *et al*., 1998) and, correspondingly, was also found to be the most significant predictor of zero counts during model development. It was determined using the Vuong test that a negative binomial model was preferred over the zero-inflated negative binomial model for the downstream migration data (Vuong test Z = 0.00, P = 0.50) and, contrastingly, the zero-inflated negative binomial model was preferred over the negative binomial model for the upstream migration data (Vuong test Z = 2.38, P <0.01). All regression statistics were completed using Stata version 11.1 (Statacorp, College Station, Texas).

Based on reviewed literature, we developed 35 candidate models for spring downstream and fall upstream migrations representing various combinations of the biologically plausible factors influencing migration. We then used an information theoretic model comparison (ITMC) technique and Akaike's Information Criterion with correction for

small sample bias (AIC_c) to identify the most parsimonious model relating environmental factors to migration (Burnham and Anderson, 2004). AIC_c is calculated as:

$$AIC_c = -2LL + 2K + 2K(K+1)/(n-K-1),$$

where *LL* is the log likelihood of the regression model, *K* is the number of parameters that are estimated in the model, and *n* is the sample size. To compare models, the parameter ΔAIC_c, or the difference in AIC_c values between a tested model and the model with the lowest AIC_c, was calculated. Models with lower ΔAIC_c values are considered a better fit to the data, however, models with ΔAIC_c values <2 are considered too similar to be ranked (Anderson *et al*., 2000). Therefore, of the models with a ΔAIC_c value <2, that which contains the fewest number of variables is considered the most parsimonious (Anderson *et al*., 2000). Furthermore, another comparison parameter, the Akaike weight (w_i), was calculated which is considered a probability measurement that a particular model (*i*) is best. Finally, evidence ratios, or the Akaike weight of the highest AIC_c model versus that of the model of interest, were calculated which represent the relative likelihood that one model is preferable to the other (Anderson *et al*., 2000). Models with high evidence ratios are not considered a good fit for the data given the selected set of models (Anderson *et al*., 2000). To order the six tested environmental factors in their relative order of importance, we summed the w_i values of all models containing a variable of interest to obtain relative importance weights. Once the most parsimonious models were selected, we used the *Z*-statistic to determine whether environmental parameters included within the model correlated significantly with eel migration. Parameters with *P*

values <0.05 were considered significant and the sign of the generated coefficients determined the directionality of each effect.

To examine correlations between amphidromous migration and diel or tidal cycles, transitions between freshwater and estuarine habitats, as detected using the flatbed antenna array system, were related to the time of sunset or high tide, respectively. A habitat transition, or migration, was considered the initial date and time that a PIT tagged eel was detected by an antenna array during the downstream or upstream migration periods. We employed circular statistical analyses to relate both diel and tidal cycles to amphidromous migrations (Batschelet, 1981). Once the time of a migratory detection was converted to hours since the previous sunset, values were then converted to an angular transformed distance from sunset ($h/24 \times 2\pi$). Similarly, once migratory detections were converted to hours since previous high tide event, values were then converted to an angular transformed distance from high tide ($h/12.4 \times 2\pi$), the denominator of which is the average time between high tide events throughout the study period. Circular statistics were then calculated including the mean vector direction (*m*), and mean vector length (*r*) and the Rayleigh test for uniformity was used to determine if migration was random with respect to diel or tidal periods (Batschelet, 1981). Test results with *P* values <0.05 were considered significant and non-random. Results for diel and tidal distributions were then compared between periods by calculating the absolute minimum circular distance from 0^{o} (i.e., sunset or high tide) and using a Kruskal-Wallis one way analysis of variance (ANOVA). Significance level was set at $P < 0.05$. When significant

differences were detected, multiple post-hoc comparisons were made using the Dunn's test. Circular statistics were calculated by hand and ANOVAs were completed using Sigmaplot 11.0 (Systat Software Inc., Point Richmond, CA, USA).

3.4. RESULTS

3.4.1. Environmental Associations of Migration

The results of the 10 best models for spring and fall amphidromous migrations, as ranked by AIC_c values, are shown in Table 3.1. For the spring downstream migration, two models contained ΔAIC_c values <2 and could not be ranked. Therefore, the model that contained the fewest number of variables was selected as the most parsimonious model which included the variables: average daily temperature (ºC) and photoperiod (h). Selection of this model was supported by the relative importance weights of included variables which were the two highest values of all six tested variables (Table 3.2). Environmental variables included within the most parsimonious model were also found to correlate significantly with migration (Table 3.3). Coefficients indicate that spring downstream migration was positively correlated with average daily temperature and negatively correlated with photoperiod. Spring downstream migration and trends in significant environmental correlates are shown in Figure 3.2 and 3.3 for 2009 and 2010, respectively. Average daily water temperature fluctuated in 2009 and 2010 years between 7.3 and 18.3 ºC. Available data indicates that average daily water temperature first exceeded 10 ºC by May 16 in 2009 and May 3 in 2010. Photoperiod increased consistently throughout the majority of the run in 2009 and the entire run in 2010.

With respect to fall upstream migration, four models were identified with ΔAIC_c values <2 and could not be ranked (Table 3.1). Therefore, the model with the fewest number of variables was selected as the most parsimonious model which included the variables: average daily temperature (ºC), average daily discharge (m^3/s) and variables describing two peaks in migration per lunar period (i.e., $\sin 2\sigma$ and $\cos 2\sigma$). The three environmental variables included in the most parsimonious model were also found to have the highest relative importance weights (Table 3.2). Although photoperiod was the next most important variable with a weight of 0.65, it was not found to be a significant predictor of migration in the top three ranked models ($P > 0.09$) and potential spurious effects relating to collinearity of average daily temperature and photoperiod during fall upstream migration further supports removal of these models from consideration. Environmental variables included within the most parsimonious model were also found to correlate significantly with migration (Table 3.3). Coefficients indicate that fall upstream migration was negatively correlated with average daily temperature, positively correlated with average daily discharge, and significantly correlated with two peaks in migration per lunar cycle. Fall upstream migration and trends in significant environmental correlates is shown in Figure 3.4. Average daily water temperature fluctuated throughout fall survey period between 4.6 and 19.9 ºC. Where migration was detected, temperatures ranged between 6.0 and 14.1 ºC. Average daily discharge fluctuated throughout fall survey period between 0.8 and 96.8 m^3/s. Where migration was detected, average daily discharge ranged between 0.8 and 52.3 m^3/s. The onset of the run was concurrent with a drop in average daily temperature to 12.6 ºC and a marked increase in average daily

discharge to 52.3 m^3/s. Peaks in migration with respect to the lunar cycle were found to occur a few days prior to new and full moons (regression line in Figure 3.5).

3.4.2. Tidal and Diel Associations of Migration

A clear relationship was identified with respect to diel timing of eel migration during spring downstream migration in 2009 and 2010 as well as fall upstream migration in 2009 (Figure 3.6). The Rayleigh test determined that all tested distributions were significantly non-random and mean vector lengths of 0.88 to 0.94 indicated strong directionality of migration time with respect to hours following sunset (Figure 3.6). The diel distribution varied significantly among the three observed migrations (Kruskal-Wallis ANOVA, $P < 0.05$). Dunn's post-hoc analysis determined that the diel distribution of the upstream migration (mean vector m=5.9 h) differed significantly from the downstream migration in 2009 (m=3.3 h) and 2010 (m=4.0 h; $P < 0.05$) as migration was concentrated earlier in the night in spring than in fall. However, the distribution of downstream migration timing did not vary significantly between years ($P > 0.05$). Although diel migration timing was found to vary by migration type, mean vectors are near the midpoint of the average period of darkness in all cases as nights are correspondingly longer in the fall (Figure 3.6).

The Rayleigh test determined that upstream migration was randomly distributed with respect to the tidal cycle in 2009 ($P > 0.05$). Contrastingly, downstream migrations were determined to be non-random with respect to the tide in 2009 and 2010 ($P < 0.05$), with mean vector directions of 3.7 h (falling tide) and 6.3 h (low tide) following high tide,

respectively (Figure 3.6). However, small mean vector lengths of 0.29 and 0.27 in 2009 and 2010, respectively, indicate a weak tidal effect. The migratory distribution with respect to tide did not vary significantly among the three observed migrations (Kruskal-Wallis ANOVA, $P = 0.05$).

3.5. DISCUSSION

3.5.1. Environmental Associations of Migration

Water temperature was found to be a significant correlate spring downstream migration of yellow eels. The direction of the regression coefficients indicates that increasing migration correlated with higher temperatures in spring. Water temperature has long been known to be a factor influencing downstream migrations in fish (Jonsson, 1991). For example, positive correlation between spring downstream migration and water temperature is well established for salmonid smolts (McCormick *et al*., 1998; Sykes *et al*., 2009). Yearly activity of yellow-stage anguillid eels, measured as catch per unit effort, has been found to be positively correlated with water temperature through studies in coastal and inland waters (Vøllestad, 1986; Jellyman, 1991; Baisez, 2001). In addition, Baisez (2001) reported increased exploratory movement in marked yellow-stage European eels with increasing spring temperatures in a freshwater marsh, followed by settling in narrow home ranges. A second exploratory phase was found to occur late in the year as temperatures decreased, after which little to no activity was shown when temperatures ranged between 6 and 12 ºC (Baisez, 2001). A negative regression coefficient indicated that photoperiod was negatively correlated with downstream

migration in the present study. However, 92% and 100% of the RST-characterized eel run in both 2009 and 2010, respectively, occurred prior to summer solstice (June 21), so photoperiod consistently increased throughout the runs. Therefore, the photoperiod effect probably reflects a correlation with time as opposed to a biological or causal function of photoperiod because the number of migrating eels consistently decreased throughout the migration period.

Temperature also correlated significantly to fall upstream migration in 2009. However, in contrast to the spring downstream migration, a negative regression coefficient indicated that migration correlated with lower temperatures in fall. Discharge also correlated significantly with migration in fall. Discharge has been shown to stimulate the upstream movement of other fish, including adult Atlantic salmon, *Salmo salar*, which rely on a minimum level of discharge to migrate upstream (Jonsson, 1991; Mitchell and Cunjack 2007) enabling passage of barriers to migration. A significant semilunar effect was identified for fall upstream migrating eels using linear-circular, or periodic regression. Peaks in migration were found to occur a few days prior to new and full moons and, although not statistically significant, a higher peak appeared to have occurred prior to the full moon. A combination of decreasing temperature and lunar cues may trigger the search for suitable overwintering habitat while increased discharge facilitates upstream movements. Full moon periods have been shown in some studies to depress anguillid eel activity (Lowe, 1952; Haraldstad *et al*., 1985), presumably an adaptation for predator avoidance during periods of high lunar illuminance. However, Cairns and

Hooley (2003) showed that even during full moon periods with low illuminance due to cloud cover, marked depression of eel activity is still apparent. The authors suggest that the observed behaviour may be due to endogenous rhythm rather than proximate lunar cues. Similar endogenous cues may be at play triggering the autumnal search for suitable overwintering habitat.

3.5.2. Tidal and Diel Associations of Migration

A clear diel pattern in migration was observed with migration almost exclusively occurring during periods of darkness. The photophobic nature of anguillid eels has been well documented (Tesch, 2003). In one study of European eels, 80% of yellow eel movements in a littoral marsh were found to occur at night (Baisez, 2001). Migration was centered about the midpoint of the dark period. This varies from a pattern observed for radio-tagged European yellow eels which exhibited increased activity in the early stages of the evening (Baras *et al*., 1998). However, the authors attributed this result to a hunger stimulus as fish presumably were not foraging since the previous sunrise (Baras *et al*., 1998).

Based on the described statistical results and observed distributions, it appears that amphidromous downstream migrations between freshwater overwintering habitat and saline summer foraging habitat are more likely to occur at periods closer to the low tide than high tide. However, low mean vector lengths indicate a weak effect and the focused diel effect of migration may have translated into a tidal effect if peaks in migration emphasized a particular tidal period that was occurring in both years. The scenario may

be further complicated for upstream-migrating eels based on the location of the antenna array. Migration within tidal waters may correlate with tide. However, the majority of the time, the antenna array is located in fresh water upstream of tidal limits and upstream-migrating eels must enter non-tidal fresh waters before passing the antenna array. If eels remain in waters downstream of the antenna array for an unknown period before moving upstream, tidal associations of migration may be masked from the current study and other factors (e.g., discharge, temperature) may be more relevant the migrations as observed. Therefore, tidal association results should be interpreted carefully. The collection of further data over multiple years and modifications to the study design for future research should clarify associations between tide and migration.

3.5.3. Conclusion

This study has shown that amphidromous migrations of yellow-stage American eels in spring and fall correlate significantly with both seasonal and diel environmental changes. Spring downstream migration from freshwater overwintering habitats to saline summer foraging habitats is predominately associated with rising water temperature. Contrastingly, fall upstream migration from saline summer foraging habitat to freshwater overwintering habitat is predominately associated with falling temperatures, increased discharge, and lunar period. Migrations in spring and fall occurred almost exclusively during periods of darkness, and weak tidal associations were identified in spring only with peaks occurring during falling and low tide periods. Examining environmental correlates of eel behaviour is a first step in identifying how environmental change

influences eel behaviour and provides insight as to the underlying causes of patterns in movement.

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Table 3.1. Summary of 10 best test models relating amphidromous migrations of yellow-stage American eels in the Upper Salmon River to environmental factors.

Model	R	AIC_c	ΔAIC_c	w_i	E.R.
Spring Migration (negative binomial models)					
Temp + Photo*	-	393.6	0.0	0.45	1.0
Temp + Photo + Lunar (2p)	-	393.8	0.2	0.41	1.1
Temp + Photo + Discharge + Lunar (1p) + Lunar (2p)	3	396.4	2.8	0.11	4.0
Photo + Discharge + Lunar (2p)	4	402.9	9.3	0.00	106.0
Photo + Discharge + Lunar (1p) + Lunar (2p)	5	404.1	10.5	0.00	193.2
Temp + Discharge + Lunar (1p)	6	404.6	11.1	0.00	251.6
Photo	7	404.9	11.3	0.00	286.6
Temp + Photo + Lunar (1p) + Lunar (2p)	8	405.0	11.4	0.00	294.0
Photo + Discharge	9	405.1	11.5	0.00	310.6
Photo + Discharge + Press + Lunar (1p) + Lunar (2p)	10	405.6	12.0	0.00	404.8
Fall Migration (zero-inflated negative binomial models)					
Temp + Photo + Discharge + Press + Lunar (2p)	-	170.9	0.0	0.25	1.0
Temp + Photo + Discharge + Lunar (2p)	-	171.1	0.2	0.23	1.1
Temp + Photo + Discharge + Press + Lunar (1p) + Lunar (2p)	-	171.9	1.0	0.15	1.6
Temp + Discharge + Lunar (2p)*	-	172.6	1.7	0.11	2.3
Temp + Discharge + Lunar (1p) + Lunar (2p)	5	173.0	2.1	0.09	2.9
Temp + Press + Lunar (2p)	6	173.5	2.6	0.07	3.7
Temp + Press + Lunar (1p) + Lunar (2p)	7	174.0	3.2	0.05	4.8
Temp + Lunar (1p) + Lunar (2p)	8	177.0	6.1	0.01	21.4
Temp + Photo + Discharge	9	177.9	7.0	0.01	33.6
Temp + Discharge	10	178.2	7.3	0.01	37.6

*Most parsimonious models, R = model rank, E.R. = Evidence Ratio, w_i = Akaike weight, Discharge = average daily discharge (m^3/s), Photo = photoperiod (h), Press = average daily atmospheric pressure (kPa), Temp = average daily temperature (ºC), Lunar (1p) indicates parameters describing one lunar peak per period (sinσ and cosσ), whereas Lunar (2p) indicates parameters describing two lunar peaks per period (sin2σ and cos2σ), where σ is the angular transformed day of the lunar cycle.

Table 3.2. Relative importance weights for environmental variables calculated for both spring downstream and fall upstream migration models.

Model	Relative Importance Weight
Spring Migration (negative binomial models)	
Photoperiod*	0.98
Average Daily Temperature*	0.98
Lunar Period (Two Peaks)	0.53
Average Daily Discharge	0.13
Lunar Period (One Peak)	0.13
Average Daily Atmospheric Pressure	0.01
Fall Migration (zero-inflated negative binomial models)	
Average Daily Temperature*	0.98
Lunar Period (Two Peaks)*	0.98
Average Daily Discharge*	0.87
Photoperiod	0.65
Average Daily Atmospheric Pressure	0.54
Lunar Period (One Peak)	0.31

*Environmental variables included within the most parsimonious models for each period.

Table 3.3. Regression outputs for the most parsimonious models relating environmental factors to amphidromous migrations.

Variable	β	SE	Z	P	95% confidence limits	
					Lower	Upper
Spring Migration Model (NBIN)						
Temperature	0.4102	0.1168	3.51	<0.001	0.1813	0.6391
Photoperiod	-2.0183	0.5463	-3.69	<0.001	-3.0889	-0.9476
Constant	27.6066	7.4400	3.71	<0.001	13.0245	42.1888
Fall Migration Model (ZINB)						
Temperature	-0.1711	0.0666	-2.57	<0.05	-0.3016	-0.0406
Discharge	0.0352	0.0139	2.53	<0.05	0.0079	0.0626
2 Lunar Peaks – sin2σ component	-0.5619	0.2326	-2.42	<0.05	-1.0179	-0.1060
2 Lunar Peaks – cos 2σ component	0.4175	0.2220	1.88	0.06	-0.0177	0.8527
Constant	2.2502	0.8174	2.75	<0.01	0.6480	3.8522
Zero-inflate variable						
Photoperiod	-4.3868	1.6367	2.1	<0.01	-7.5947	-1.1789
Constant	50.3574	18.6178	7.3	<0.01	13.8672	86.8475

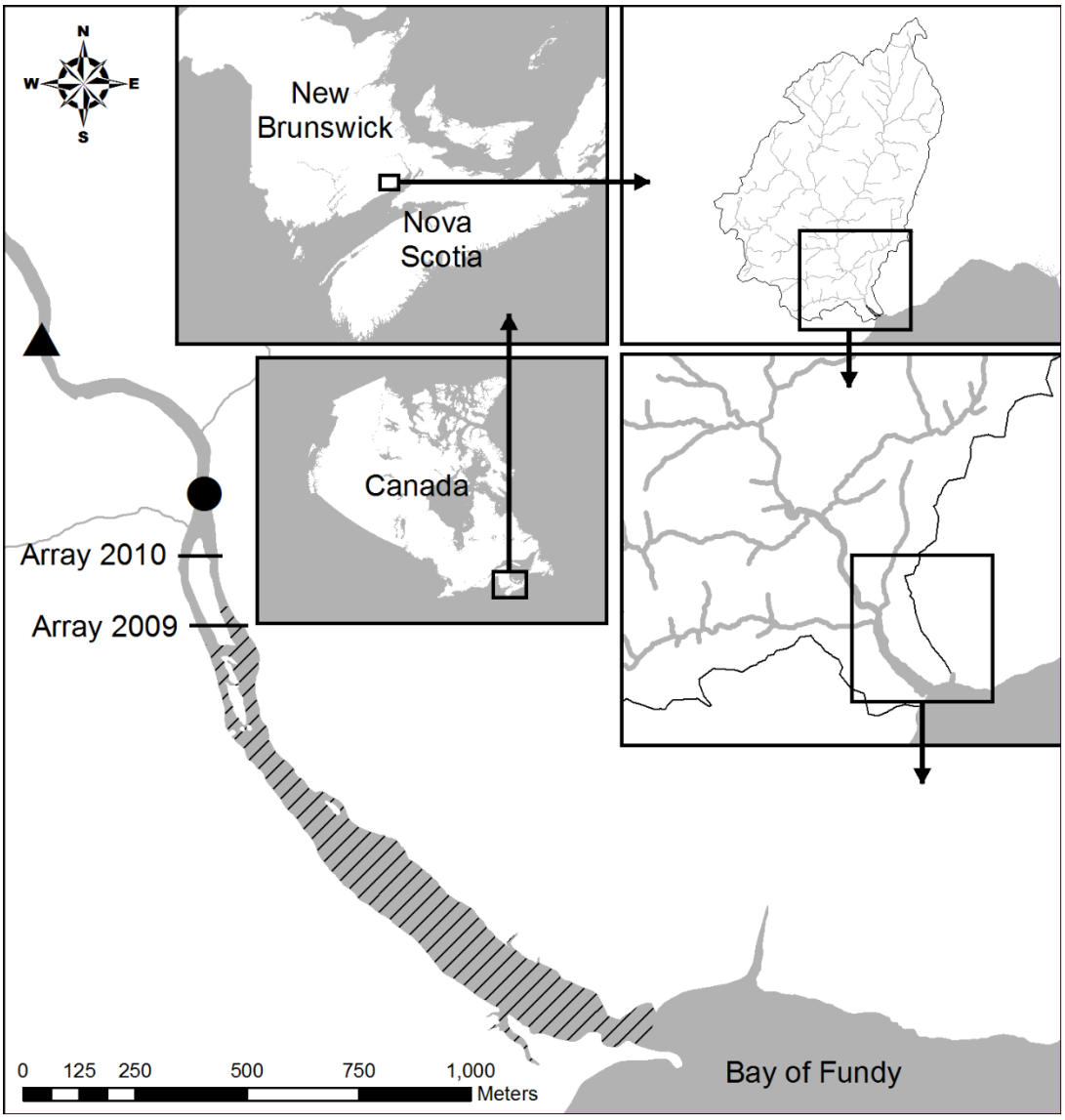


Figure 3.1. Map of the Upper Salmon River in New Brunswick, Canada. The capture location (black circle), release location (black triangle), and locations of the PIT antenna array in 2009 and 2010 are shown. The hatched area of the river represents the estuary or saline-influenced area of the river.

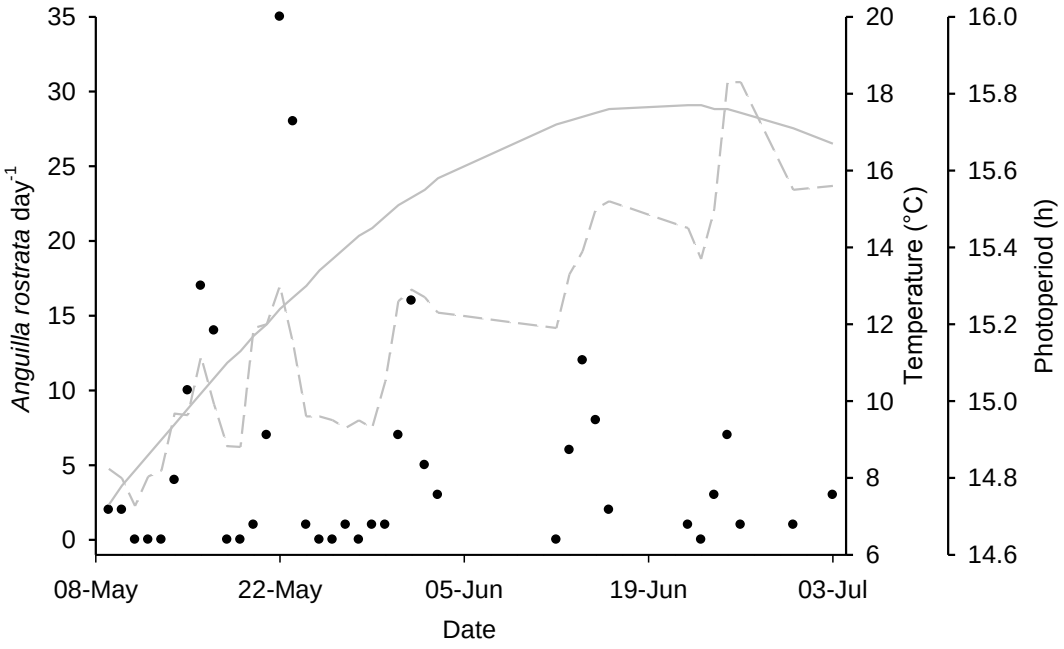


Figure 3.2. Spring downstream migration of yellow stage American eels in the Upper Salmon River in 2009. Black dots represents the number eels migrating per day as measured by rotary screw trap catch. Environmental parameters which significantly correlated with migration are also plotted including temperature (dashed line) and photoperiod (solid line).

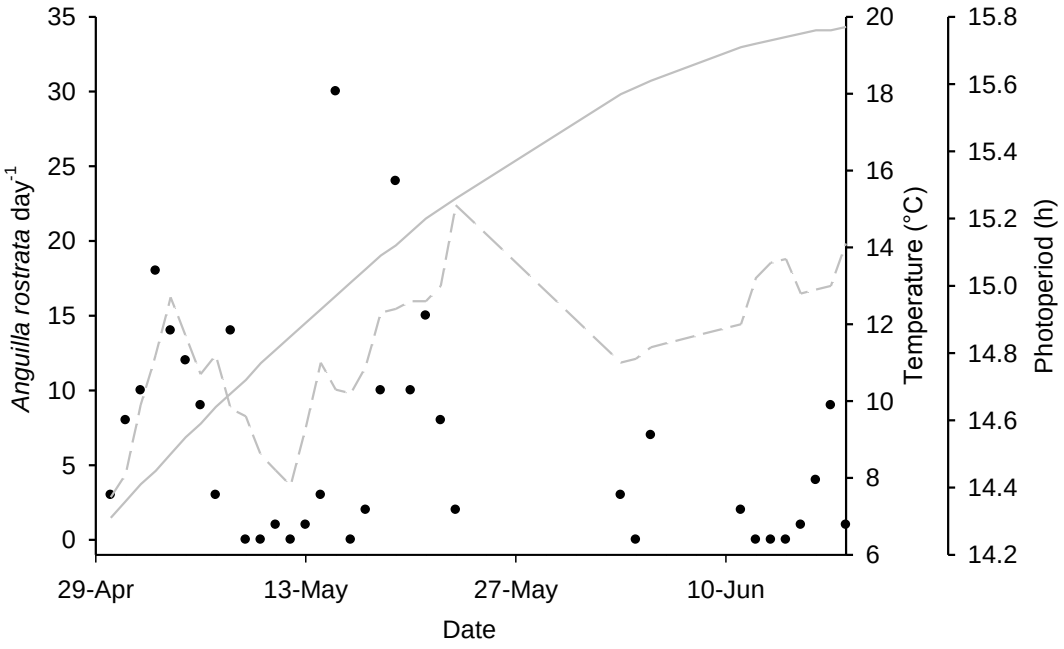


Figure 3.3. Spring downstream migration of yellow stage American eels in the Upper Salmon River in 2010. Black dots represents the number eels migrating per day as measured by rotary screw trap catch. Environmental parameters which significantly correlated with migration are also plotted including temperature (dashed line) and photoperiod (solid line).

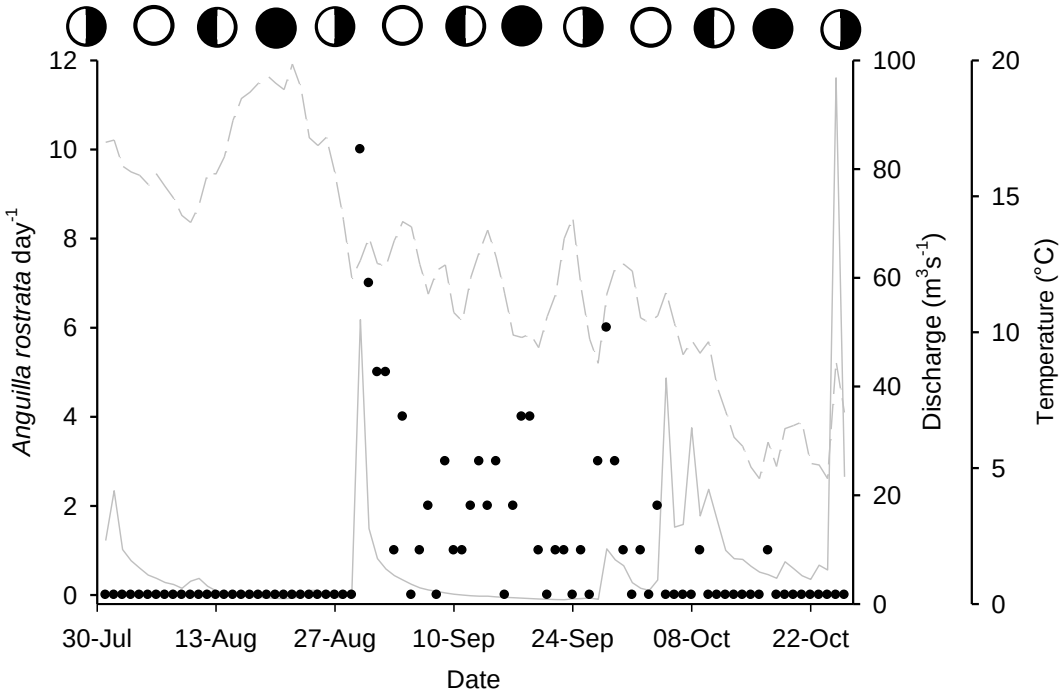


Figure 3.4. Fall upstream migration of yellow stage American eels in the Upper Salmon River in 2009. Black dots represents the number eels migrating per day as measured using a passive integrated transponder array. Environmental parameters which significantly correlated with migration are also plotted including temperature (dashed line), discharge (solid line), and lunar phase (circles above graph). Full, half-filled, and empty circles indicate new, quarter, and full moon, respectively.

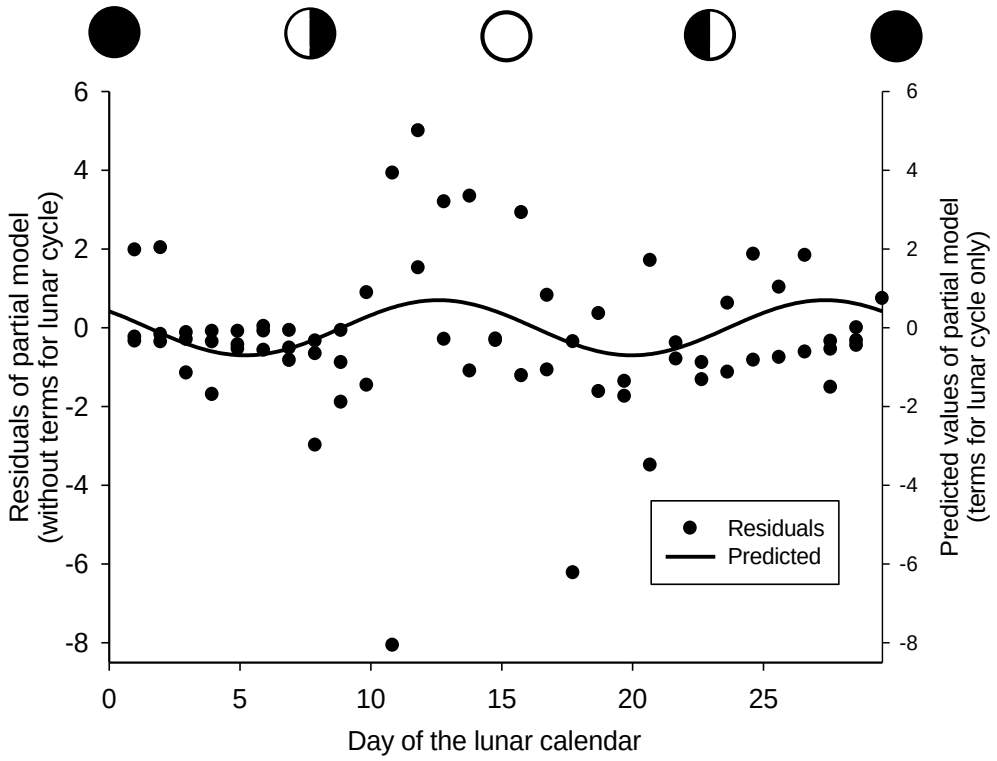
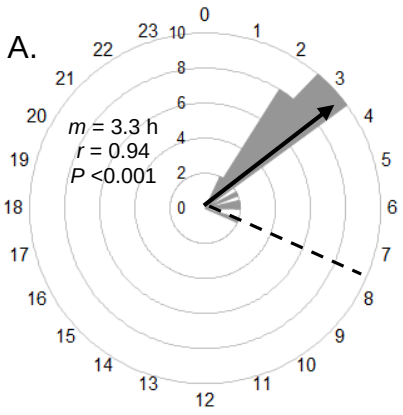
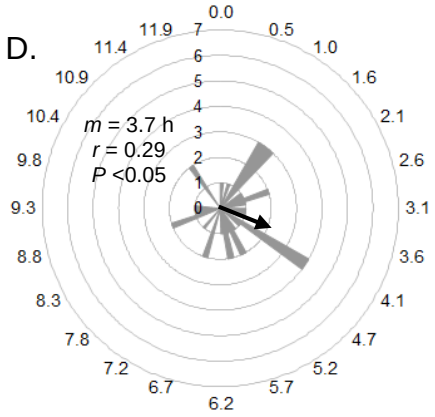
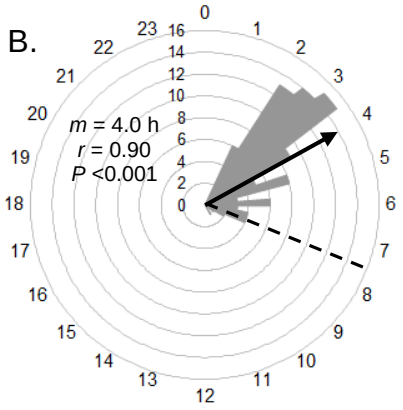


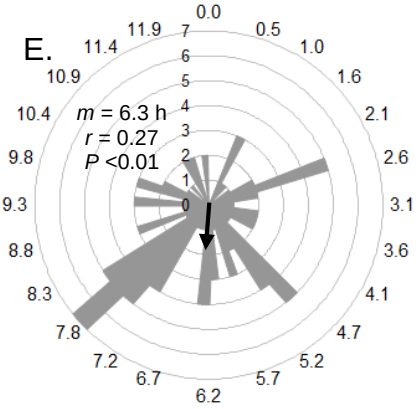
Figure 3.5. Relationship between lunar period and the upstream migration of yellow stage American eels in fall 2009. Residuals were calculated by subtracting, from the observed number of migrating eels, the numbers predicted using a partial zero-inflated negative binomial model that included all terms from the most parsimonious model, excluding the lunar variables (i.e., $\sin 2\sigma$ and $\cos 2\sigma$). The dots represent observed residuals and the solid line represents prediction of the partial model including the lunar variables only. Full, half-filled, and empty circles indicate new, quarter, and full moon, respectively.

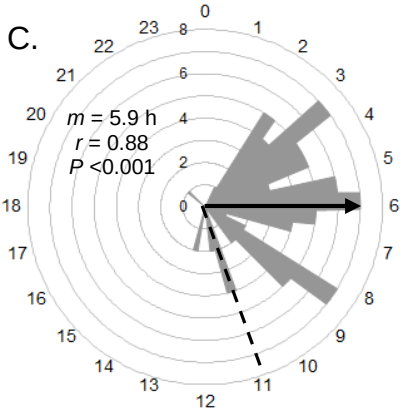
Figure 3.6. Polar histograms of total number of initial detections by migrating American eels at the passive integrated transponder antenna array in relation to hours post-sunset (left column, sunset = 0) and hours post-high tide (right column, high tide = 0). The upper row (a, d) represents eels detected during downstream migration in 2009, the middle row (b, e) represents eels detected during downstream migration in 2010, and the lower row (c, f) represents eels detected during upstream migration in fall 2009. Diel and tidal histograms are divided by 30 and 15 minute intervals, respectively. The black arrows are mean vectors of m-direction and r-length (plotted as a proportion of the circular plot radius). P values denote significance from the Rayleigh test for circular uniformity. Dashed lines indicate the average time of sunrise for the observed periods.

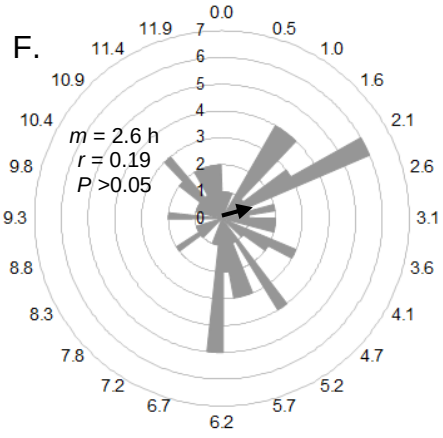

A.
m = 3.3 h
r = 0.94
P <0.001


D.
m = 3.7 h
r = 0.29
P <0.05


B.
m = 4.0 h
r = 0.90
P <0.001


E.
m = 6.3 h
r = 0.27
P <0.01


C.
m = 5.9 h
r = 0.88
P <0.001


F.
m = 2.6 h
r = 0.19
P >0.05

4. Run-size quantification and biological characteristics of spring-migrating yellow-stage American eels (*Anguilla rostrata*) in the Upper Salmon River, New Brunswick, in 2009 & 2010

4.1. ABSTRACT

The recent decline in American eel abundance in the upper St. Lawrence River and Lake Ontario has highlighted an urgent need for information relating to the current status of the American eel in Canada. Enumerating spring migrating yellow-stage American eels in riverine systems may provide a robust monitoring tool for trends in total population status and such activities could be implemented in conjunction with existing rotary screw trap (RST) monitoring programs for Atlantic salmon. We characterized migrating yellow eels in the Upper Salmon River during the springs of 2009 and 2010 using an RST and two fyke nets. A mark-recapture experiment was completed to estimate the number of downstream migrating eels using a Bayesian model. Estimates of migrating eel abundance for eels $\geq$20 cm in total length were 10,220 (97.5% CI: 6139-16,540) and 3022 (97.5% CI: 2158-5073) in 2009 and 2010, respectively. The fyke nets and RST were found to sample contrasting components of the migrating eel population. An RST retention test determined that eels <20.6 cm in length were more likely to escape the RST holding box, probably due to gaps between the holding box and the debris wheel. In contrast, the fyke nets did not appear efficient in capturing larger eels (i.e., >20 cm).

RST modifications are warranted in order to increase the capture efficiency for small-bodied fish.

4.2. INTRODUCTION

The American eel, *Anguilla rostrata*, has encountered population-wide declines in step with other species of freshwater eels belonging to the family Anguillidae (Dekker et al. 2003). The status of the American eel in Canada is of particular concern due to the precipitous declines in abundance that have occurred in the upper St. Lawrence River and Lake Ontario (Castonguay et al. 1994, Casselman et al. 1997, Casselman, 2003). As a result, the recommended status of the American eel has been changed from Special Concern to Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012).

The ecological importance of the American eel varies greatly with different life stages. Anguillid eels are proficient colonizers, opportunistic feeders, and eventually top predators in later life stages, thus playing an important role in ecosystems (Tesch 2003). The American eel is particularly important to aboriginal peoples and has provided a commercial and recreational fishery in Canada with annual harvests ranging between 500 and 1200 t between 1961 and 2003 (DFO 2010). However, harvests have declined from approximately 1100 t in the late 1980s to approximately 500 t in 2003 and the most recent estimate for 2007 places annual harvest at 459 t (DFO 2010). The majority of fishing activities in Canada has historically occurred in the St. Lawrence River system

and tidal waters of the Gulf of St. Lawrence (Cairns et al. 2008). The recent declines, coupled with a general lack of knowledge regarding the American eel's life cycle and behaviour, has highlighted the need for robust monitoring programs designed to measure abundances and trends in American eel populations using mathematical models (Haro et al. 2000).

A large volume of data relating to American eel fisheries and scientific surveys in Canada is available and provides useful information in trends of abundance over time (Cairns et al. 2007, Cairns et al. 2008). However, American eel fisheries do not present a robust monitoring tool for yellow-stage eels due to fishery closures in the upper St. Lawrence River and Lake Ontario in 2004 as well as varying demand for yellow eels in Québec and Atlantic Canada (COSEWIC 2012). Monitoring techniques that do not shift with market demand are ideal. Electrofishing surveys document valuable information in estimating relative freshwater abundances of American eels over long time periods. However, obtaining accurate numerical abundance estimates of American eels through depletion-method electrofishing, as is done for Atlantic salmon, may be difficult for eels as captures are usually low in number and shocked eels may be confined to the substrate crevices in which they hide during the day. Electrofishing may also cause sublethal injuries in American eels due to the occurrence of tetany and internal injury at required power levels (Reynolds and Holliman 2004). Further study regarding American eel abundance estimates via electrofishing techniques is required. A promising new method for monitoring trends in American eel abundance in navigable waters including lakes, large

pools, and estuaries may be through the implementation of a recently-developed glass-bottom boat survey (Cairns et al. 2009 Hallet 2013).

It has been shown that rotary screw traps (RST) are a valuable tool in monitoring a number of fish species which move through rivers in addition to salmonids (Chaput and Jones 2004). Enumerating migrating yellow-stage American eels using current RST monitoring programs may provide a valuable and easily implemented tool for obtaining accurate year to year abundance estimates for migrating eels using mark and recapture techniques. The presence of migrating American eels in rivers monitored using RSTs appears widespread in Atlantic Canada and Québec (Caron and Gauthier 2003, Chaput and Jones 2004, Caron et al. 2005, Flanagan et al. 2006, Cairns et al. 2007, Clément et al. 2007, Thibault et al. 2007, Breau et al. 2010). However, it is unknown how efficient rotary screw traps are at capturing migrating American eels and what component of the migrating populations are currently being caught. The current study is part of a detailed examination of migrating eels in the Upper Salmon River, New Brunswick. An ongoing Atlantic salmon smolt monitoring program, using a RST to capture spring-migrating smolts, is conducted in the Upper Salmon River by Fundy National Park of Canada staff as a part of their Atlantic salmon conservation efforts. Our goal was to characterize spring-migrating eels using the park-operated RST, and additional fyke nets, and to assess the applicability of Atlantic salmon smolt monitoring techniques for migrating yellow-stage American eels.

4.3. METHODS

4.3.1. Study Area

The Upper Salmon River (45º36'N, 64º56'W) is located in southeastern New Brunswick and drains into the Chignecto Bay inlet of the Inner Bay of Fundy (Figure 4.1). At its lower reaches, the Upper Salmon River is bordered by Fundy National Park of Canada to the west and the village of Alma to the east. Although the lower 13 km of the river are bordered by Fundy National Park, the upper reaches of the watershed are outside of park boundaries and are subjected to significant forestry harvest (Parks Canada 1997). With a drainage basin of 177 km^2, the watershed has an average slope of 10.9% (Figure 4.2). The lower 8 km of the main channel above the head of tide is separated from its tributaries by a number of waterfalls and is comprised of mainly boulder-strewn habitat and fast-flowing waters.

4.3.2. Field Operations

All field activities were completed in the spring and early summer of 2009 and 2010. Capture methods and trap locations did not vary between years. A 1.52 m diameter RST was installed approximately 200 m upstream of the head of tide in a relatively deep and fast-flowing area of the river (Figure 4.1, 4.3a; see Chaput and Jones (2004) for a detailed description of RST design and operation). The RST was held in place by an overhead cable and its position could be adjusted, when needed, to maximize capture efficiencies. The RST could generally be accessed on foot depending on water levels; however, an inflatable raft was used during extreme discharge events.

In addition to the RST, two fyke nets were installed approximately 150 m upstream of the head of tide (Figure 4.1, 4.3b). The nets consisted of two 8.5 m wings that were directed at a 45º angle to the mouth of the net in order to target downstream-migrating fish. The wings and body of the nets were made with 10 mm mesh and the cod-end was comprised of 6 mm mesh. The body of the trap was 3.4 m in length and 0.6 m in diameter. The fyke nets covered most of the river width but were spaced by approximately 25 m of river length wherein fish could swim between the two nets. One fyke net, FN1, was installed on the west side of the river in an area approximately 0.2 m shallower than the location of the other fyke net, FN2 (Figure 4.1). The fyke nets were anchored to the substrate using three 1.5 m pieces of size 30M rebar, one located at the mouth of the body and one at the end of each of the two wings which were hammered in place (i.e., between the crevices of boulders) using a sledge hammer (Figure 4.3b; n.b., nets were red-flagged as a safety precaution). To further stabilize the nets against the current, two 1.5 m pieces of 25M rebar were installed 0.5 m upstream of the wing anchors and the two rebar were tied together using rope. To increase capture efficiency of the fyke nets, the lower part of the wings, including the weighted line, were made flush to the substrate by lifting any small boulders beneath the wings and placing them on top of the net. Current deflection by the fyke wings directed water flow toward the mouth of the trap. The body of the trap was extended downstream of the mouth by the current and no further anchoring was needed. The cod-end of the trap was tied using a small length of rope and this ensured that no fish could escape and that the trap was then "set". As the trap was only tied to the anchored rebar, it was easily removed when needed and the rebar could be left in place undamaged

until the next fishing event. Depending on the amount of debris, fyke nets were cleaned 1-2 times a week to ensure that they didn't become damaged due to increased current resistance.

Both the RST and fyke nets were checked once daily, in the morning. All bycatch was identified to species, counted, recorded, and released immediately at the capture location. All Atlantic salmon were given to Fundy National Park for further processing in relation to their monitoring program or released as bycatch when directed by their group.

Operating conditions of the RST and fyke nets in 2009 and 2010 are summarized in Table 4.1. The RST was set continuously for the first six weeks of activities in 2009 and only partially set for the final two weeks (Figure 4.4). In 2010, the RST was set continuously for the first five weeks of activity but was raised five days in June due to an extreme discharge event (Figure 4.5). The only time that the RST became jammed with debris was during this event. Low discharge levels in 2009 may have decreased the capture ability of the RST for two periods ranging between June 4 to June 11 and June 17 to June 21 as the RST drum ceased rotating occasionally in these periods (Figure 4.4). To increase the capture efficiency of the RST in 2010, a plywood barrier was added to the left side of the river on May 9 to increase flow to the RST. The RST was observed to have stopped turning completely due to low discharge levels on the mornings of May 24 to June 2, 2010 (Figure 4.5). Fyke nets were set 4-5 days a week in 2009 and continuously set throughout 2010. However, nets were damaged and removed for 10 days due to the high discharge event in June of 2010.

Water temperature was measured using temperature dataloggers (VEMCO Minilog©) either attached to the RST or tied to a piece of rebar hammered into the substrate between the two fyke nets. Missing water temperature values in the first two weeks following RST installation in 2009 were predicted using a temperature datalogger installed near the mouth of a Kinnie Brook, adjacent to the capture area (i.e., within 80 m). A linear regression using: discharge (i.e., in the Upper Salmon River), photoperiod, minimum, maximum, and average atmospheric temperature, and precipitation as independent variables was completed to describe known average daily river temperature values throughout the 2009 run period ($R^2 = 0.86$, n = 115, $p < 0.0001$) and then missing values were predicted using the resulting regression equation. Mean daily discharge (m^3/s) was calculated for the Upper Salmon River by multiplying mean discharge values of the adjacent Point Wolfe River by 1.22 as the discharge in the two rivers have been found to be highly correlated (Matthew Smith, GIS Specialist, Fundy National Park of Canada, personal communication). Discharge values in the Pointe Wolfe River were obtained from Environment Canada Hydrographic Station 01BV006 and are measured in real-time using a pressure actuated bubbler gauge transmitter (Hydrologic Alphé 3030, Grenoble, France) coupled to a data logger/transmitter (Sutron 8210, Sterling, VA, USA).

4.3.3. Sampling and Marking Procedures

All captured American eels were anaesthetized in a solution of tricaine methanesulphonate (MS-222; Argent Laboratories, Redmond VA) and water (250 ppm) until a loss of state of immobility was observed, then weighed in air (0.1 g) using an

electronic balance and measured for total length (0.1 cm). Three marking procedures were utilized and the procedures varied in use by year and by eel size.

Firstly, in both 2009 and 2010, all eels ≥25 cm in total length were marked using a 23 mm glass encapsulated passive integrated transponder (PIT) tag [Texas Instruments (TIRIS™) model RI-TRP-RRHP, 134.2 kHz] surgically implanted into the abdominal cavity following the protocol of Roussel et al. (2000). The incision area was sealed using a single drop of n-butyl cyanoacrylate (Vetbond™ surgical glue) to reduce tag loss and promote healing. Secondly, during the 2009 field season, all eels ≥20 cm in total length were marked using a 12.5 mm glass-encapsulated PIT tag (Biomark model TX1411SST, 134.2 kHz) inserted beneath the skin using a PIT tag injector consisting of a 12 gauge hypodermic needle and push rod. These tags were implanted as a part of Fundy National Park of Canada's American eel scientific program. The PIT tag was placed inside the needle and the needle was inserted beneath the skin towards the anterior end of the eel beginning at the dorsal fin origin. To ensure sufficient tag retention, the needle was inserted at least 25 mm, or twice the length of the PIT tag, before ejecting the tag and removing the needle in one fluid motion. Tissue samples were collected from all PIT tagged eels for stable isotope analysis relating to a complementary study and, therefore, tagged eels were additionally marked by a pectoral fin clip. All PIT tagging equipment was disinfected using 70% isopropyl alcohol between tag events. Finally, all untagged eels captured in 2010 were marked by pectoral fin clipping in the same manner as PIT

tagged eels in order to increase the sample size by marking eels smaller than 20 cm in total length.

All procedures were carried out according to the Canadian Council on Animal Care guidelines and were approved by the Animal Care Committee of both the University of New Brunswick (Protocol # 09043/10003) and Fisheries and Oceans Canada Maritimes Region (Protocol # 09-11). Approximately 20% and 17% percent of American eels tagged in 2009 and 2010, respectively, were held in live boxes as controls for 10 ten days prior to release to determine tag retention and handling mortality. Tag retention in controls was 100% and no adverse effects relating to tagging and/or fin clipping were identified.

4.3.4. Run Size Estimates

Population of migrating yellow-stage American eels was estimated from mark and recapture experiments. Marked eels were carried approximately 600 m upstream of the RST in water backpacks and released. As it was determined that eels <20 cm in total length were less likely to be retained by the RST (see RST Retention Test Results), abundance estimates were only completed for eels $\geq$20 cm and mark-recapture data inputs were sorted accordingly. Mark-recapture data were analyzed with WinBUGS (Imperial College and the Medical Research Council, UK) using an aggregated Bayesian model assuming a binomial distribution for the catches (Gazey and Staley 1986). A survival rate of 100% was assumed based on control holds and observed tag retention. Changes in trap capture efficiencies likely varied over time with changes in discharge,

temperature, and run timing. However, recaptures were not high enough to use a stratified estimation model (Arnason et al. 1996).

4.3.5. Trap Comparisons

For each year, mean length and mean weight of yellow eels caught by the RST and two fyke nets were compared using a one-way ANOVA followed by Tukey's HSD post-hoc test. All ANOVAs were completed using Systat 11 software (Systat Software Inc., Chicago, IL, USA). Data were log-transformed (base 10) and the assumptions of ANOVA were met.

To determine if the size of migrating eels differed with time, a linear regression was completed using length and calendar date as dependent and independent variables, repsectively. Regressions were completed for total catch, RST catch, and fyke net catch in 2009 and 2010. Regressions were completed using Systat 11 software (Systat Software Inc., Chicago, IL, USA).

RST Retention Test

To examine the ability of the RST to retain captured American eels, 62 different yellow eels, ranging in length between 10.7 and 33.9 cm, were placed in the RST holding box in three separate overnight trials on the nights of June 2, 15, and 17, 2009 (using 28, 20, and 14 eels, respectively). Prior to placement in the RST, eels were marked using an electronic hot branding device (Gemini Cautery System CP70-1700). A hot brand was used to scar eel skin near the dorsal fin origin in order to distinguish test eels from newly

captured eels. Due to the small size of eels and inability to visually identify brand-shapes in the resulting scars, individual eels were identified the following day based on a combination of scar presence and size (i.e., length and weight) which was variable enough to enable re-identification of individual eels on the following day. The RST was fished following approximately 20 hours of holding and eels were re-identified to calculate trap retention. To determine if length or weight had an effect on RST retention, logistic regressions using length or weight as the dependent variable and retention (1) vs. escape (0) as the independent variable were completed using Stata 11 Software (StataCorp LP, College Station, TX, USA).

4.3.6. Biological Characteristics

Between-year comparisons of mean length and mean weight of yellow eels were completed using t-tests which were performed using Systat 11 software (Systat Software Inc., Chicago, IL, USA). Length and weight data were log-transformed prior to completing t-tests and all t-test assumptions were met. To determine if the condition of yellow eels varied between years, log-length and log-weight relationships were compared using an Analysis of Covariance (ANCOVA) with year as the covariate. The ANCOVA was completed using Systat 11 software (Systat Software Inc., Chicago, IL, USA).

4.4. RESULTS

Mean daily water temperature varied over the study years between 7.3 and 18.3 ºC (Table 4.1). Mean daily water temperature had already exceeded 10 ºC when the data logger

was installed in 2009 on May 20 (Table 4.1). However, manual daily temperature measurement indicated that water temperatures exceeded 10 ºC by at least May 17. The first day mean daily water temperature was ≥10 ºC in 2010 was on May 3 (Table 4.1). Atmospheric temperature, measured at the Fundy National Park monitoring station, averaged 6.8 ºC in the first two weeks of May, 2009, and 9.8 ºC in the first two weeks of May, 2010.

4.4.1. Run Timing

No yellow eels were captured during the first 24 hours of RST operation in 2009, however, 3 eels were captured during this period in 2010 (Table 4.2). The date of median catch (when 50% of the run's catch was obtained, excluding recaptures; values are unadjusted with respect to variation in fishing effort or trap efficiency) was on May 27 in 2009 and May 10, 2010 (Table 4.2). In 2009 and 2010, 90% of the run's catch was obtained within 41 and 44 days, respectively (Table 4.2, 4.3, 4.4).

4.4.2. Run Size Estimates

A total of 382 and 242 marked eels ≥20 cm were carried and released 600 m upstream of the RST in 2009 and 2010, respectively during the mark-recapture periods (Table 4.5). The time to recapture of PIT tagged eels varied between 1 and 19 days in 2009 and 3 and 12 days in 2010 (Appendix 1). The percentages of eligible marked eels (i.e., ≥20 cm) recaptured by the fyke nets and RST were 7% and 17% in 2009 and 2010, respectively.

The mark-recapture period in 2009 was between May 5 and July 3 (Table 4.5). The aggregated Bayesian model determined an estimated run size of 10,220 yellow eels ≥20 cm in length (95% C.I. 6139 to 16,540; Table 4.5; Figure 4.6). Both the capture efficiency of the RST and fyke nets were found to be 2.1% (95% C.I. 1.2% to 3.3% for both).

The mark-recapture period in 2010 was between April 29 and June 6 (Table 4.5). Mark-recapture activities were shortened in 2010 as eels captured after June 1 (n = 56) were held for the RST retention test (Table 4.4). A run size of 3022 yellow eels ≥20 cm (95% C.I. 2158 to 5073) was determined using the aggregated Bayesian model for 2010 (Table 4.5; Figure 4.6). The capture efficiency of the RST was found to be 6.8% (95% C.I. 4.3% to 9.8%) and the capture efficiency of the fyke nets was found to be 2.3% (95% C.I. 1.4% to 3.4%).

There were seven and two yellow eel mortalities in 2009 and 2010, respectively. With the exception of one eel in both years, all mortalities were a result of complications relating to surgical implantation of PIT tags or sacrifice due to parasitic infection (Table 4.3, 4.4).

4.4.3. Biological Characteristics

Between-year comparisons of biological characteristics of captured yellow eels are shown in Table 4.6. There was no significant difference in the mean log-transformed

length (t-test, df=1198, t=0.844, p=0.406) or mean log-transformed weight (t-test, df=1198, t=1.454, p=0.146) of eels capture in 2009 and 2010 (Table 4.6).

The average daily length (total) of migrating yellow-stage American eels fluctuated between 16.6 and 29.1 cm in 2009, and 13.3 and 28.0 cm in 2010, when the catch of all traps were combined and there was no significant trend in size with respect to time (Figure 4.7). However, a significant inverse trend in eel size with respect to time of capture was identified for the fyke nets and RST in and 2010, wherein the RST was found to catch smaller eels as time progressed and the fyke nets were found to catch larger eels as time progressed (Figure 4.7). Size was not significantly related to date for either gear in 2009 (Figure 4.7).

The results of the ANCOVA determined that the length-to-weight relationships differed significantly between years ($F_{(1, 1194)} = 15.80$, $p < 0.001$) such that eels in 2009 were 0.01 g heavier at a given length than in 2010 (Figure 4.8).

4.4.4. Trap Comparisons

The proportion of total catch caught by each trap varied with time. The shallower-installed fyke net, FN1, was found to capture the largest proportion of migrating eels early in the run and the smallest proportion as the run progressed in both years (Figure 4.4, 4.5). The deeper-installed fyke net, FN2, was more consistent with slightly increased proportion occurring in middle of the run in 2010 when discharge levels were the lowest observed in both years (Figure 4.4, 4.5). The RST was relatively constant in the

proportion of total catch through time and appeared to correlate with the sum of the catch for fyke nets FN1 and FN2 with the exception of reduced discharge events that likely affected the capture ability of the RST thus decreasing catch (Figure 4.4, 4.5).

Significant differences between traps with respect to log-transformed eel length and log-transformed eel weight were found in both years (Table 4.7). Post-hoc comparisons determined that the mean length and weight of eels captured in all three traps in 2009 and 2010 differed significantly (Tukey's HSD, $P<0.05$) with the largest eels being captured by the RST, followed by eels captured in FN2, and the smallest eels were captured in FN1 (Table 4.7). Total length distributions show that fyke nets and the RST are sampling different components of the migrating eel population based on size (Figure 4.9, 4.10).

RST Retention Test

The RST retention test identified a clear trend of yellow eel retention with respect to length and weight of test eels (Figure 4.11). Logistic regression determined that 86% and 90% of retention by the RST holding box can be explained by either length or weight models, respectively (Table 4.8, 4.9). Based on the logistic regression models, it was determined that eels <20.6 cm in length or <11.48 g in weight were more likely to escape the holding box than to be retained within it (i.e., $Pr(y=1) <0.50$; Figure 4.11).

4.4.5. Trap Bycatch

In addition to the 771 American eels, six other species were captured using the fyke nets over the study period, including 135 Atlantic salmon (*Salmo salar*; 129 smolts and 6

parr), 8 brook trout (*Salvelinus fontinalis*), 3 rainbow smelt (*Osmerus mordax*), 2 fourspine sticklebacks (*Apeltes quadracus*), and 2 blacknose dace (*Rhinichthys atratulus*).

In addition to the 429 American eels, 7 other species were captured using the park-operated RST throughout the study period including 2545 Atlantic salmon (*Salmo salar*), 5 brook trout (*Salvelinus fontinalis*), 1 American shad (*Alosa sapidissima*), 1 rainbow smelt (*Osmerus mordax*), 2 fourspine sticklebacks (*Apeltes quadracus*), 3 alewife (*Alosa pseudoharengus*), and 3 blacknose dace (*Rhinichthys atratulus*). It was determined that 5.3% of migrating Atlantic salmon captured by all 3 traps in 2009 and 2010, were captured by the fyke nets.

4.5. DISCUSSION

Due to the low catch obtained within the first week following installation of the RST in 2009, it is quite likely that the run was in the beginning stages and the entire period of the run was characterized. However, although the RST was installed a week earlier in 2010, a significant peak in migration occurred within the first week following installation and, therefore, the extent of migration prior to monitoring activities is unknown and the run size may be underestimated as a result.

Observed difference in proportion of total catch over time for the two fyke nets suggest that yellow eels migrating earlier in the season do so in the shallower side of the river in

the area of FN1 and as the season progresses, more migration occurs in the deeper side of the river where FN2 was installed.

The retention test results show a clear bias in RST captures towards eels >20.6 cm. This value is expected to vary greatly by RST and may vary between years for a single RST if holding box assembly results in changes to gap-size. Although it cannot be determined whether trap inefficiencies or differences in sub-populations of yellow-stage American eels account for variations in the sizes retained by RSTs in monitoring programs, variations have been observed. For example, an RST on the Restigouche River, New Brunswick, in 2003 captured a high proportion of eels in the 15-20 cm range (Chaput and Jones 2004). Contrastingly, a low proportion of eels in the 15-20 cm range was captured on the Saint Jean River in 2002 (Caron and Gauthier 2003). Eels were observed in the current study exiting the holding box through a small corner-hole where the base of the trap meets the debris wheel. Adjustments to the RST should be made to minimize any such gaps in order to retain small-bodied fish. In addition, upon examining the size distribution of yellow eels captured by the fyke nets compared to those captured with the RST, it appears that the nets themselves are not efficient at capturing large eels. Differences in the capture efficiencies of the fyke nets and RST were also observed with respect to migrating Atlantic salmon. The fyke nets were not efficient in capturing migrating Atlantic salmon compared to the RST. Absence of large-sized eels in the fyke nets, and the reduced capture efficiency for Atlantic salmon smolts when compared to the RST, may share a common explanation, but this is beyond the scope of the current study.

Biases demonstrated by both traps highlight the benefit of using more than one capture method in describing a population of fish.

Run size estimates in both years show that thousands of yellow eels are migrating downstream in the Upper Salmon River during spring. Estimates of the number of migrating eels in the Upper Salmon River is an incremental step towards determining the extent of migrating eels in Canada and their relative importance to the greater population. Such migrations are not unique to the Bay of Fundy as a mark-recapture study on the Saint-Jean River, Québec estimated, using a RST, that between 18,000 and 36,000 eels were migrating downstream in spring (Caron and Gauthier 2003; Caron et al. 2005).

Abundance estimates in both years were only for eels $\geq$20 cm in length. These eels represented only 54% and 49% of the total catch in 2009 and 2010, respectively. In addition, the mark-recapture period in 2010 was cut short due to the RST retention test and there is a high degree of uncertainty with respect to characterization of the early stages of the run due to immediate captures upon installation of the RST. These reasons may explain why a markedly smaller estimate was obtained in 2010 than in 2009. Capture efficiencies of the fyke nets were found to be very consistent between years. However, the capture efficiency of the RST more than tripled in 2010. This is likely related to low discharge levels in 2010 during the peak migration period which increased the proportion of the river width that was fished by the RST. The variation observed in fyke net capture over time emphasizes the importance of using stratified Bayesian models due to the variation in capture efficiency of traps over time. Future studies of migrating

yellow eels should attempt to increase the capture efficiency or number of released and eligible eels in order to obtain enough data to use a stratified Bayesian model. Ensuring that the RST can sample small-bodied fish and, thus, include a larger component of the migrating population in the abundance estimate would be one way of increasing the robustness of the mark-recapture experiment. As PIT tags could not be inserted into eels <20 cm in length, a method for marking small eels that would allow indication of the release period would also be beneficial. Further studies should focus on the utility of such methods as hot or cold branding (Sorensen et al. 1983) and visible implant elastomer (VIE; Skinner et al. 2006) for marking small yellow eels in mark-recapture studies.

Other studies examining migrating eels using RSTs have shown that migrating populations are biologically similar across different systems and are typically small in size as found in the current study. Cairns et al. (2007) displays length frequency distributions of RST-captured eels in Southern Gulf of St. Lawrence Rivers, indicating that the majority of spring migrating American eels in the Miramichi River and Restigouche River, New Brunswick, as well as the Margaree River, Nova Scotia, are between 10 and 40 cm in length. Similarly, the majority of migrating eels in the Saint-Jean River ranged in length between 20 and 35 cm in 2002 and 2004 (Caron and Gauthier 2003; Caron et al. 2005).

This study has demonstrated that methods for quantifying migrating salmonids can be applied to migrating yellow-stage American eels in order to obtain reliable annual

estimates of abundance. Protocols for monitoring salmonids could be adjusted to improve characterization of migrating yellow eels, including modification of the RST to improve capture efficiency for small-bodied fish, and incorporation of different marking techniques to improve mark-recapture estimates with minimal impact to marked eels. Recommendations may also be applicable to characterizing migrations of sea lamprey (*Petromyzon marinus*), another species exhibiting anguilliform locomotion.

4.6. ACKNOWLEDGEMENTS

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Table 4.1. Summary of field operations of the rotary screw trap (RST), and fyke nets (FN1 and FN2) in the Upper Salmon River in 2009 and 2010.

	Year	
	2009	2010
RST operation start date	May 5	April 29
RST operation end date	July 3	June 18
Number of days RST not operating (i.e., jammed or raised)	8	5
FN1 operation start date	May 13	May 3
FN1 operation end date	July 3	June 18
Number of days FN1 not operating	19	10
FN2 operation start date	May 13	May 3
FN2 operation end date	July 3	June 18
Number of days FN2 not operating	19	10
Mean daily water temperature range (°C)	7.3 to 18.3	7.5 to 16.1
First day when mean temperature ≥10°C	May 20*	May 3
Eels ≥200 mm tagged with 12.5 mm PIT tag (Biomark)	Yes	No
Eels ≥250 mm tagged with 23 mm PIT tag (Aquartis)	Yes	Yes
Untagged eels marked with right pectoral fin clip	No	Yes

* Water temperature already exceeding 10 °C when data logger was installed (11.9°C).

Table 4.2. Run timing of yellow-stage American eels in the Upper Salmon River during 2009 and 2010.

	Year	
	2009	2010
Catch of American eels on the first day of operation	0	3
Date of first capture	May 7	April 30
Date of 5th percentile of catch	May 14	May 3
Date of median catch	May 27	May 10
Date of 95th percentile of catch	June 23	June 15
Date of last catch	July 3	June 18

Table 4.3. Summary of capture and release activities for all yellow eels in the spring of 2009. Days in which a trap was not operating are indicated by "-".

	First-Time Captures													Recaptures		
	Catch				Tagged (PIT)			Mortality		Released*						
Date	Total	RST	FN1	FN2	Total Tagged	12.5 mm	23 mm	Capture	Post Capture	Not Marked	Tagged	Total		RST	FN1	FN2
06-May	0	0	-	-	0	0	0	0	0	0	0	-		-	-	-
07-May	1	1	-	-	1	1	1	0	0	0	0	0		0	-	-
08-May	0	0	-	-	0	0	0	0	0	0	0	0		0	-	-
09-May	2	2	-	-	2	2	2	0	0	0	0	0		0	-	-
10-May	2	2	-	-	2	2	2	0	0	0	0	0		0	-	-
11-May	0	0	-	-	0	0	0	0	0	0	0	0		0	-	-
12-May	0	0	-	-	0	0	0	0	0	0	0	0		0	-	-
13-May	0	0	-	-	0	0	0	0	0	0	4	0		0	-	-
14-May	32	4	23	5	9	9	9	0	0	23	6	0		0	0	0
15-May	53	10	25	18	26	26	12	0	3†	24	20	0		0	0	0
16-May	17	17	-	-	17	17	12	0	0	0	0	0		0	-	-
17-May	14	14	-	-	14	14	7	0	0	0	0	0		0	-	-
18-May	0	0	-	-	0	0	0	0	0	0	27	0		0	-	-
19-May	2	0	1	1	2	2	0	0	0	0	2	1		1	0	0
20-May	15	1	13	1	7	7	3	0	0	8	7	0		0	0	0
21-May	41	7	29	5	17	17	8	0	0	24	15	0		0	0	0
22-May	138	35	90	13	64	64	22	0	0	74	60	0		0	0	0
23-May	28	28	-	-	28	28	9	0	0	0	0	0		0	-	-
24-May	1	1	-	-	1	1	1	0	0	0	0	0		0	-	-
25-May	2	0		2	2	2	0	0	0	0	36	0		0	0	0
26-May	3	0	1	2	0	0	0	0	0	3	2	0		0	0	0
27-May	6	1	4	1	1	1	1	0	0	5	3	0		0	0	0
28-May	5	0	4	1	1	1	0	0	2‡	2	1	0		0	0	0
29-May	11	1	6	4	2	2	0	0	0	9	2	1		0	0	1
30-May	1	1	-	-	1	1	0	0	0	0	0	0		0	-	-
31-May	7	7	-	-	7	7	2	0	0	0	0	0		0	-	-
01-Jun	89	16	3	70	58	58	19	0	0	31	62	5		1	0	4
02-Jun	7	5		2	6	6	2	0	0	1	6	1		0	0	1
03-Jun	7	3	2	2	4	4	2	0	0	3	4	0		0	0	0
04-Jun	9	4	3	2	4	4	2	0	0	5	5	1		1	0	0
05-Jun	14	0	8	6	4	4	1	0	0	10	4	0		0	0	0
06-Jun	0	0	-	-	0	0	0	0	0	0	0	0		0	-	-
07-Jun	0	0	-	-	0	0	0	0	0	0	0	0		0	-	-
08-Jun	42	0	0	42	24	24	4	0	0	18	25	0		0	0	0
09-Jun	8	0	0	8	4	4	2	0	0	4	4	0		0	0	0
10-Jun	9	0	2	7	4	4	0	0	0	5	4	0		0	0	0
11-Jun	3	0	0	3	1	1	0	0	0	2	4	0		0	0	0
12-Jun	18	0	0	18	13	13	5	0	0	5	12	1		0	0	1
13-Jun	6	6	-	-	6	6	4	0	0	0	0	2		2	-	-
14-Jun	12	12	-	-	12	12	9	0	0	0	0	1		1	-	-
15-Jun	32	8	5	19	19	19	10	0	0	13	31	0		0	0	0
16-Jun	12	2	4	6	6	6	2	0	0	6	4	0		0	0	0
17-Jun	9	0	1	8	1	1	0	0	0	8	1	0		0	0	0
18-Jun	7	0	2	5	4	4	1	0	0	3	7	1		0	1	0
19-Jun	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
20-Jun	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
21-Jun	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
22-Jun	4	1	0	3	2	2	2	0	0	2	4	1		1	0	0
23-Jun	4	0	2	2	0	0	0	0	0	4	0	0		0	0	0
24-Jun	5	3	0	2	2	2	0	1	1‡	1	2	0		0	0	0
25-Jun	10	7	1	2	7	7	0	0	0	3	11	0		0	0	0
26-Jun	12	1	8	3	4	4	1	0	0	8	4	0		0	0	0
27-Jun	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
28-Jun	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
29-Jun	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
30-Jun	1	1	0	0	0	0	0	0	0	1	0	0		0	0	0
01-Jul	0	-	-	-	0	0	0	0	0	0	0	0		-	-	-
02-Jul	0	-	-	-	0	0	0	0	0	0	1	0		-	-	-
03-Jul	4	3	0	1	3	3	2	0	0	1	3	0		0	0	0
Total	705	204	237	264	392	392	159	1	6	306	383	15		7	1	7

* 7 PIT tagged and 2 untagged eels escaped live boxes at unknown dates. † Eels sacrificed due to complications related to surgical implantation of 23 mm PIT tag. ‡ Eels sacrificed due to visually observed parasitic infection.

Table 4.4. Daily yellow eel catch in the Upper Salmon River during spring downstream migration in 2010. Days in which a trap was not operating are indicated by "-".

	First-Time Captures										Recaptures		
	Catch				Tagged (PIT)			Mortality		Released*			
Date	Total	RST	FN1	FN2	Total	Tagged 12.5 mm	Tagged 23 mm	Capture	Post	Not Marked	Tagged Total	RST	FN1	FN2
30-Apr	3	3	-	-	0	0		0		0	0	0	-	-
01-May	8	8	-	-	0	0		0		0	0	0	-	-
02-May	10	10	-	-	0	0		0		0	0	0	-	-
03-May	18	18	-	-	0	0		0		0	0	0	-	-
04-May	72	14	42		111	75		0		75	29	0	0	0
05-May	76	12	54		76	66		0		66	8	0	0	0
06-May	24	9	11		24	16		0		16	7	0	0	0
07-May	14	3	6	5	14	12		0		0	0	1	0	0
08-May	18	14	0		18	13	5	0	1†	25	5	6	0	1
09-May	1	0	0	1	1	1		0		0	0	0	0	0
10-May	5	0	3		5	5		0		5	0	5	0	0	0
11-May	3	1	1	1	3	3		0		3	0	0	1	0
12-May	4	0	4		3	3		1		3	0	0	1	0
13-May	1	1	0		1	0	1	0		0	1	1	0	0	0
14-May	4	3	1		4	2		0		0	0	0	0	0
15-May	35	30	0	5	36	18		0		0	0	4	0	0
16-May	1	0	1		1	1		0		21	17	0	0	0
17-May	6	2	3	1	6	6		0		6	11	0	0	0
18-May	14	10	0		14	7	7	0		7	6	1	0	1
19-May	33	24	6		33	14		0		11	15	1	0	1
20-May	25	10	2		25	20	5	0		20	4	1	0	0
21-May	18	15	0		18	7		0		7	9	0	0	1
22-May	12	8	1		12	11	1	0		0	0	2	0	0
23-May	2	2	0		2	1	1	0		0	0	0	0	0
24-May	4	0	4		4	4		0		16	1	0	0	0
25-May	11	0	3		11	11		0		11	0	0	1	0
26-May	4	0	0		4	3	1	0		3	5	0	0	0
27-May	3	0	0		3	3		0		0	0	0	0	0
28-May	1	0	1		1	1		0		0	0	0	0	0
29-May	2	0	0		2	2		0		0	0	0	0	0
30-May	2	0	1	1	2	2		0		0	0	0	0	0
31-May	5	0	1		5	5		0		9	0	0	0	0
01-Jun	15	0	2		15	10	5	0				0	0	0
02-Jun	4	1	3		4	2		0				0	0	0
03-Jun	3	3	0		3	3		0				0	0	0
04-Jun	0	0	0		0	0		0				0	0	0
05-Jun	7	7	-	-	7	5		0				1	-	-
06-Jun	0	0	-	-	0	0		0				0	-	-
07-Jun	-	-	-	-	-	-	-	-	-			-	-	-
08-Jun	-	-	-	-	-	-	-	-	-			-	-	-
09-Jun	-	-	-	-	-	-	-	-	-			-	-	-
10-Jun	-	-	-	-	-	-	-	-	-			-	-	-
11-Jun	2	2	-	-	2	2		0				0	-	-
12-Jun	0	0	-	-	0	0		0				0	-	-
13-Jun	0	0	-	-	0	0		0				0	-	-
14-Jun	0	0	-	-	0	0		0				0	-	-
15-Jun	10	1	7		10	9	1	0				0	0	0
16-Jun	5	4	1		5	3		0				0	0	0
17-Jun	9	9	0		9	9		0				0	0	0
18-Jun	1	1	0		0	0		0				0	0	0
Total	495	225	158		494	355		1	1	304	118	17	3	4

* Due to a shift in activities starting on June 1st, a total of 70 captured eels (22 tagged and 48 clipped) were not recycled 500 m upstream. 62 of these eels were utilized for the RST retention test, 7 were utilized for Fundy National Park interpretive programs, and 1 eel escaped from a holding box near the site of capture. † Eels sacrificed due to complications related to surgical implantation of 23 mm PIT tag

Table 4.5. Mark and recapture data inputs and results using an aggregated Bayesian model in 2009 and 2010 to estimate trap capture efficiencies and abundance of migrating yellow-stage American eels in the Upper Salmon River. All values and final estimates are for eels >20 cm only in both years in specified periods. The total eligible eels for recapture were not adjusted for mortality based on high survival and tag retention of control eels.

Model Parameters

	2009	2010
Tagging period	May 13 to Jul 3	May 4 to May 31
Recapture period	May 14 to Jul 3	May 5 to Jun 6
Total marked eels released	382	242
Total first-time RST captures	200	213
Total RST recaptures	7	17
Total first-time fyke net captures	203	73
Total fyke net recaptures	8	4

Bayesian Estimates

		Mode	2.5^{th} percentile	97.5^{th} percentile	Coefficient of variation
2009	Run size*	10,220	6139	16,540	26%
	RST efficiency	2.1%	1.2%	3.3%	
	Fyke nets efficiency	2.1%	1.2%	3.3%	
2010	Run size*	3022	2158	5073	23%
	RST efficiency	6.8%	4.3%	9.8%	
	Fyke nets efficiency	2.3%	1.4%	3.4%	

* *N.B.* Abundance estimates are for specified periods only and only a sub-component of migrating eels (>20 cm) were eligible for estimation. As such, values in this table are inconsistent with those of Tables 3 and 4, which summarize the capture and fate of all yellow eels in 2009 and 2010.

Table 4.6. Between-year comparisons of biological characteristics of yellow-stage American eels captured in the Upper Salmon River in 2009 and 2010.

		Length (mm)					Weight (g)				
Year	n	Min	Max	Mean	CI	SD	Min	Max	Mean	CI	SD
2009	705	11.2	58.2	21.9	0.4	5.5	1.7	410.0	16.5	1.5	20.9
2010	495	10.7	52.5	21.7	0.5	5.8	1.4	186.8	15.7	1.5	16.7
		Log_{10} Length (mm)					Log_{10} Weight (g)				
Year	n	Min	Max	Mean	CI	SD	Min	Max	Mean	CI	SD
2009	705	1.05	1.76	1.33^{A}	0.01	0.10	0.24	2.61	1.08^{A}	0.02	0.32
2010	495	1.03	1.72	1.32^{A}	0.01	0.11	0.13	2.27	1.05^{A}	0.03	0.34

N.B. CI = 95% Confidence Interval, SD = One Standard Deviation. Different letters indicate significant difference in between years (t-test, P <0.05).

Table 4.7. Between trap comparisons of mean length and weight of yellow-stage American eels captured in the Upper Salmon River in 2009 and 2010.

Year	Trap	n	Length (mm)			Weight (g)		
			Mean	CI	SD	Mean	CI	SD
2009	RST	204	26.0	0.6	4.2	24.9	0.6	17.3
	FN1	237	18.9	0.6	4.5	10.5	0.6	11.9
	FN2	264	21.3	0.6	5.2	15.4	0.6	26.9
2010	RST	255	25.8	0.6	4.9	24.1	0.6	20.7
	FN1	158	17.8	0.6	3.7	7.9	0.6	6.2
	FN2	112	19.0C	0.8	4.2	9.9	0.8	8.1
Year	Trap	n	Log_{10} Length (mm)			Log_{10} Weight (g)		
			Mean	CI	SD	Mean	CI	SD
2009	RST	204	1.41^{A}	0.01	0.07	1.34^{A}	0.03	0.21
	FN1	237	1.27^{B}	0.01	0.09	0.90^{B}	0.04	0.28
	FN2	264	1.32^{C}	0.01	0.10	1.04^{C}	0.04	0.30
2010	RST	255	1.40^{A}	0.01	0.08	1.30^{A}	0.03	0.26
	FN1	158	1.24^{B}	0.01	0.08	0.81^{B}	0.04	0.25
	FN2	112	1.27^{C}	0.02	0.09	0.90^{C}	0.05	0.27

N.B. RST = rotary screw trap, FN1 = Fyke Net 1, FN2 = Fyke Net 2, CI = 95% Confidence Interval, SD = One Standard Deviation. Different letters indicate significant difference in trap means within a given year (ANOVA, $P < 0.05$).

Table 4.8. Results of the logistic regression relating RST retention to length.

Model Parameters						
Predictor Variable	β	*SE* β	*Z*	*df*	*P*	e^{β}
Length	1.41	0.53	2.67	1	0.008	4.104
Constant	-29.03	11.10	-2.62	1	0.009	N/A
Evaluations						
			χ^2	*df*	*P*	
Overall model evaluation						
Likelihood ratio test			72.24	1	0.000	
Goodness of Fit Tests						
Hosmer & Lemeshow			1.25	8	0.996	
Pearson χ^2			12.60	48	1.000	

N.B. e^{β} = odds ratio. The pseudo R^2 value for the model was 0.86.

Table 4.9. Results of the logistic regression relating RST retention to weight.

Model Parameters						
Predictor Variable	β	*SE* β	*Z*	*df*	*P*	e^{β}
Weight	1.05	0.45	2.34	1	0.019	2.871
Constant	-12.11	5.55	-2.18	1	0.029	N/A
Evaluations						
			χ^2	*df*	*P*	
Overall model evaluation						
Likelihood ratio test			75.68	1	0.000	
Goodness of Fit Tests						
Hosmer & Lemeshow			1.93	8	0.983	
Pearson χ^2			9.43	60	1.000	

N.B. e^{β} = odds ratio. The pseudo R^2 value for the model was 0.90.

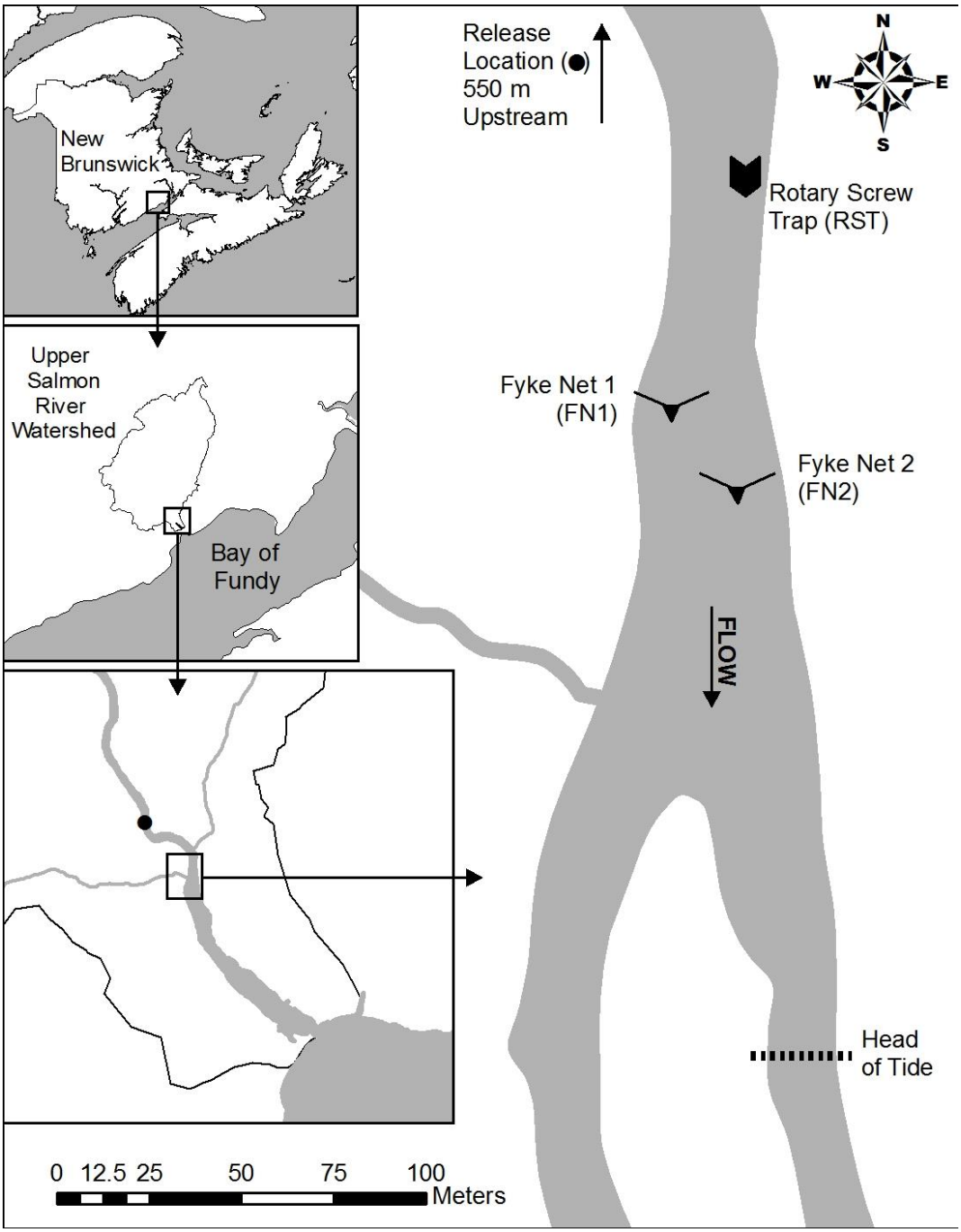

Figure 4.1. Site schematic of the Upper Salmon River in New Brunswick, Canada illustrating the locations of traps in 2009 and 2010. The release location, where marked American eels were recycled in the mark-recapture experiments, is also indicated (black circle).

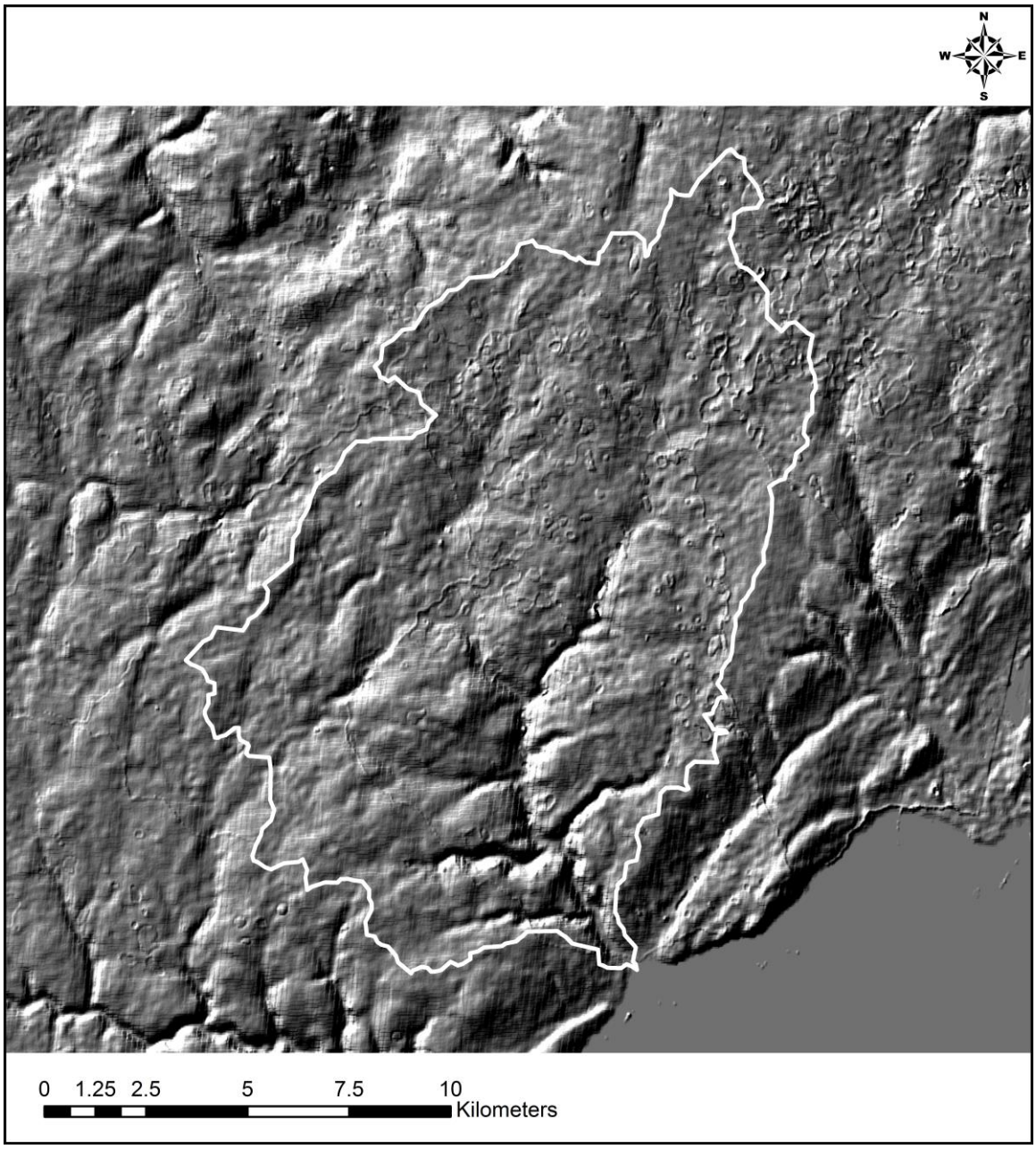

Figure 4.2. Relief schematic of the Upper Salmon River watershed (white line), New Brunswick, Canada. The lower 13 river kilometres of the main stem is characterized by a high slope compared to the upper reaches. Digital elevation model provided by NASA's Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER).

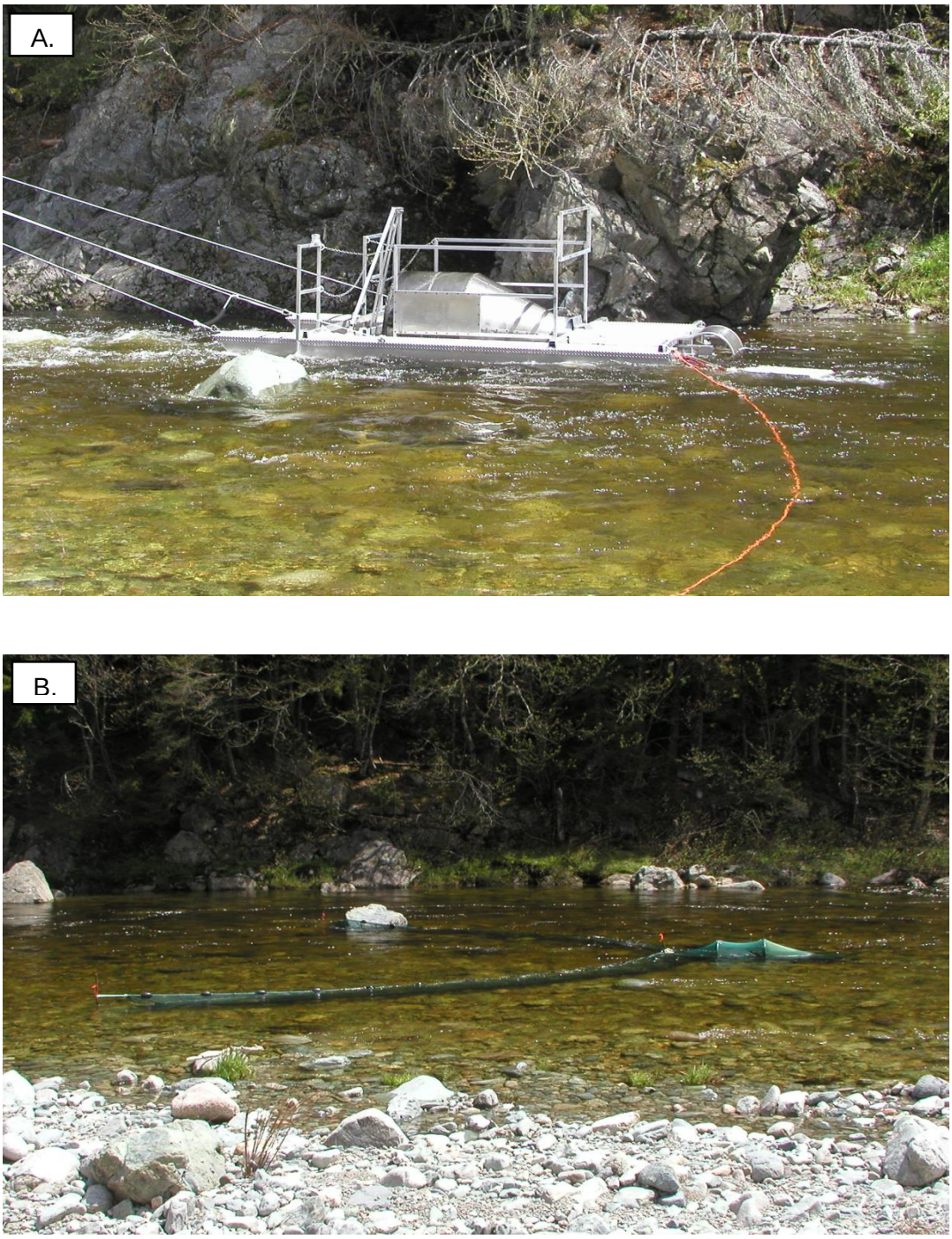

Figure 4.3. Side views of a) the rotary screw trap and b) fyke net 1 while operating in the Upper Salmon River in the spring of 2009.

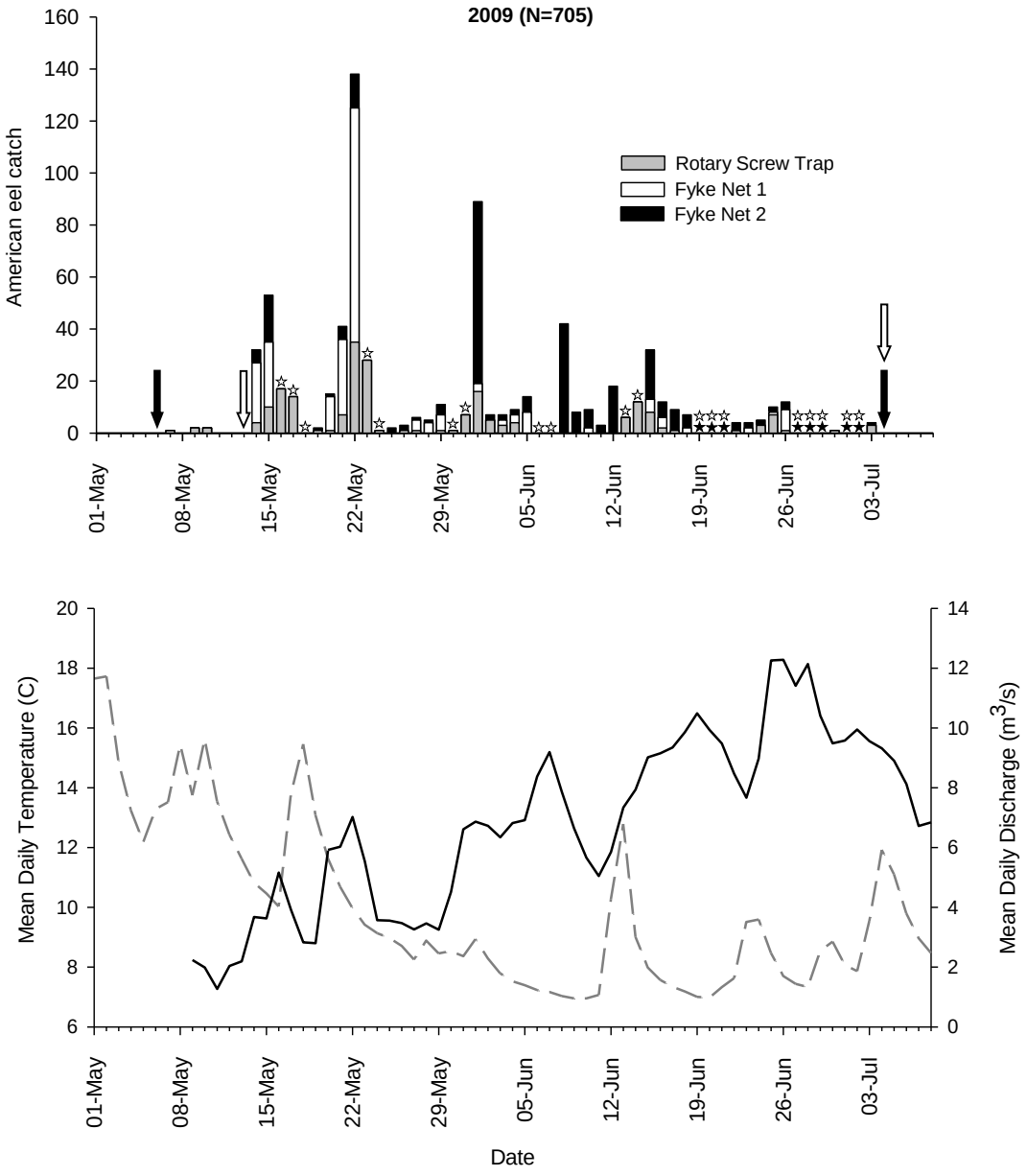

Figure 4.4. Daily catch, and proportion by trap, of American eels (upper panel) as well as mean daily water temperature (lower panel; solid line) and discharge (lower panel; dashed line) in the Upper Salmon River in 2009. Installation and removal dates are indicated for the rotary screw trap (filled arrows) and fyke nets (empty arrows) as well as dates in which the rotary screw trap (filled stars) and fyke nets (empty stars) were not set. Vertical dotted lines indicate periods in which low discharge levels are believed to have affected RST operability.

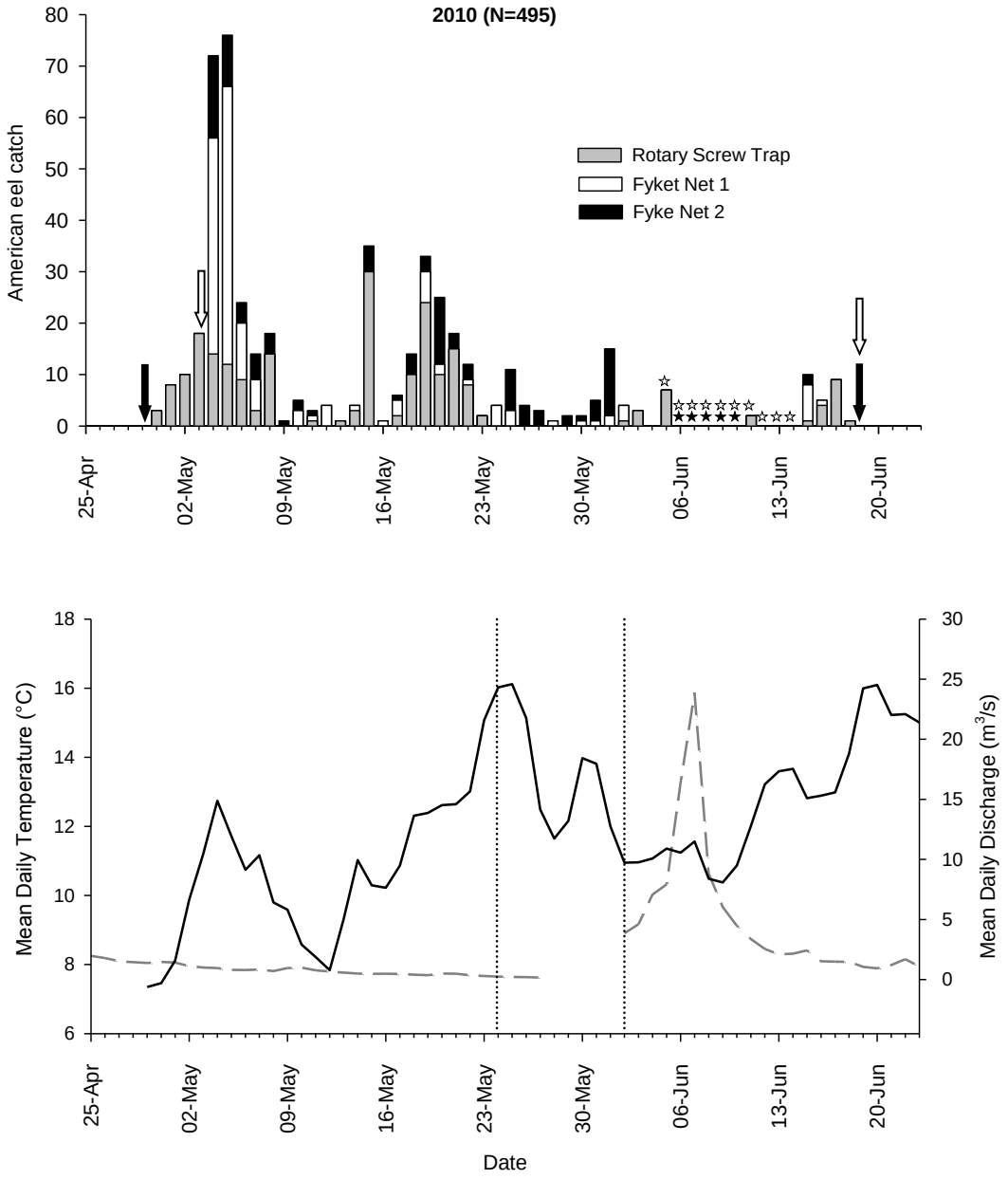

Figure 4.5. Daily catch, and proportion by trap, of American eels (upper panel) as well as mean daily water temperature (lower panel; solid line) and discharge (lower panel; dashed line) in the Upper Salmon River in 2010. Installation and removal dates are indicated for the rotary screw trap (filled arrows) and fyke nets (empty arrows) as well as dates in which the rotary screw trap (filled stars) and fyke nets (empty stars) were not set. Vertical dotted lines indicate periods in which low discharge levels are believed to have affected RST operability.

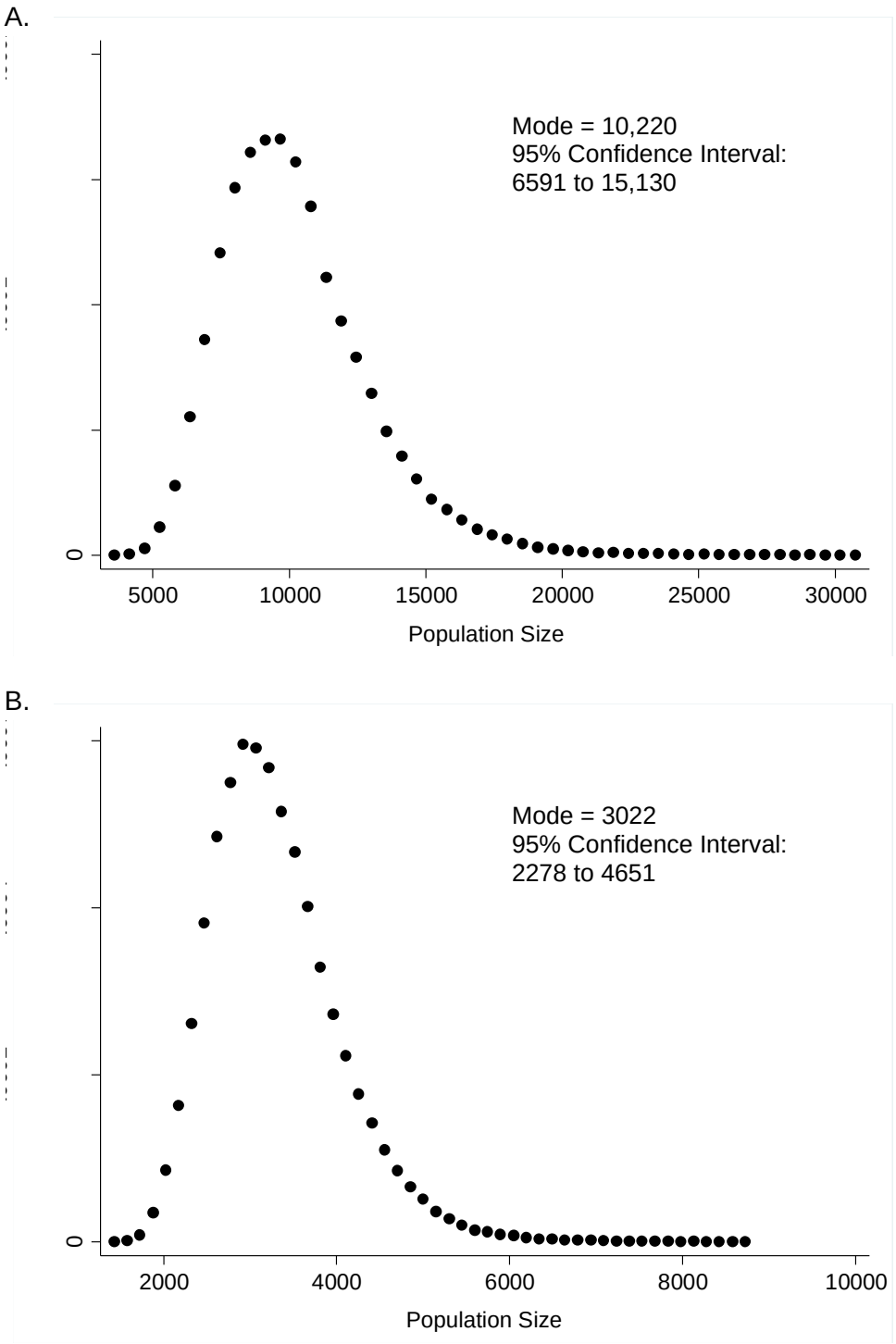

Figure 4.6. Probability profiles from Bayesian estimates of the run size of yellow-stage American eels (≥20 cm total length) in the Upper Salmon River in a) 2009 and b) 2010.

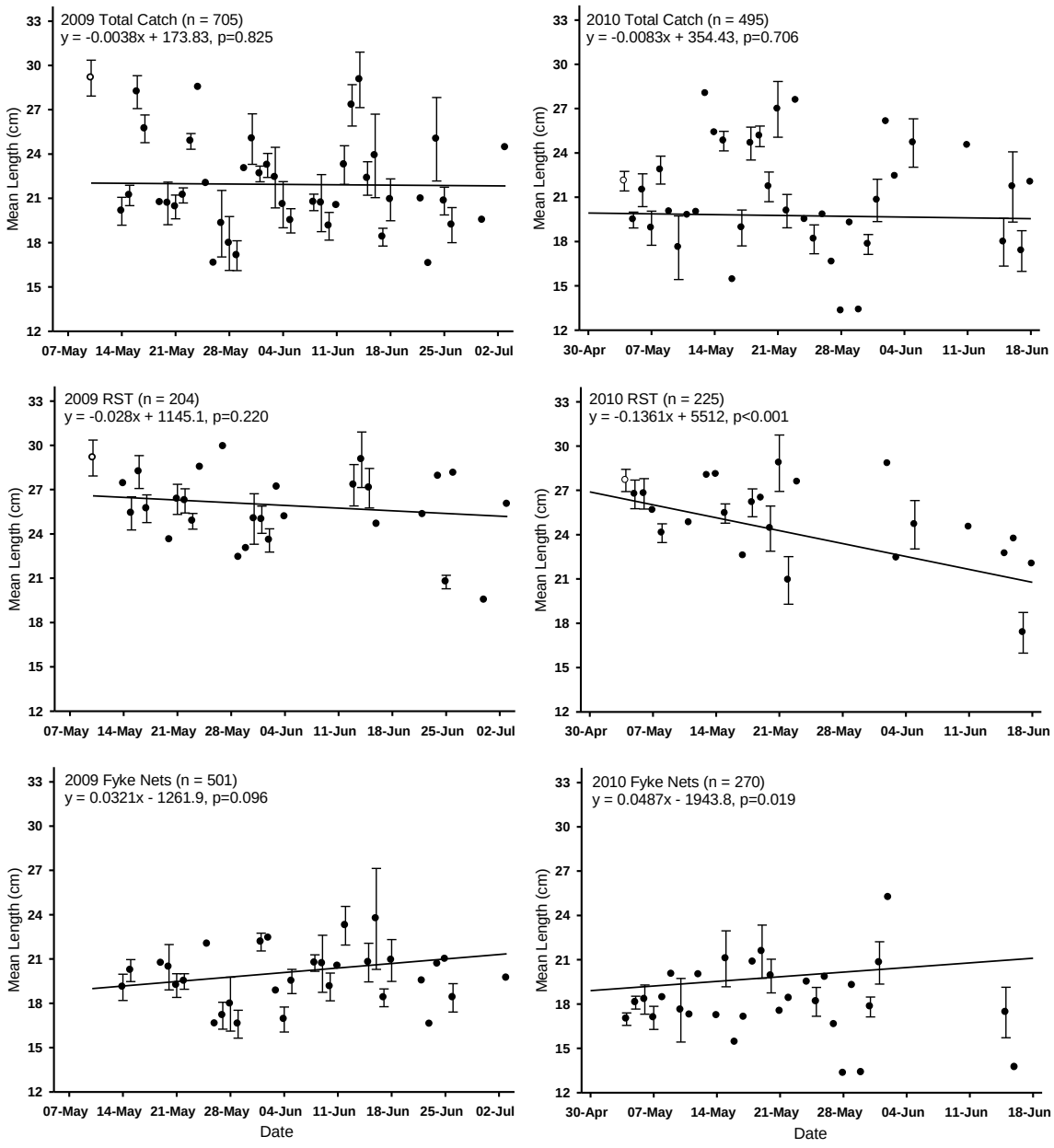

Figure 4.7. Daily mean total length (± one standard error) of American eels captured in the Upper Salmon River in 2009 (left column) and 2010 (right column). Results are shown for total catch (top row), rotary screw trap only (middle row), and fyke nets only (bottom row). Standard error of the mean is not indicated for days when n <5 eels. Empty circles represent pooled values for the previous 3 days catch. Regression lines, equations, and associated p-values are also presented.

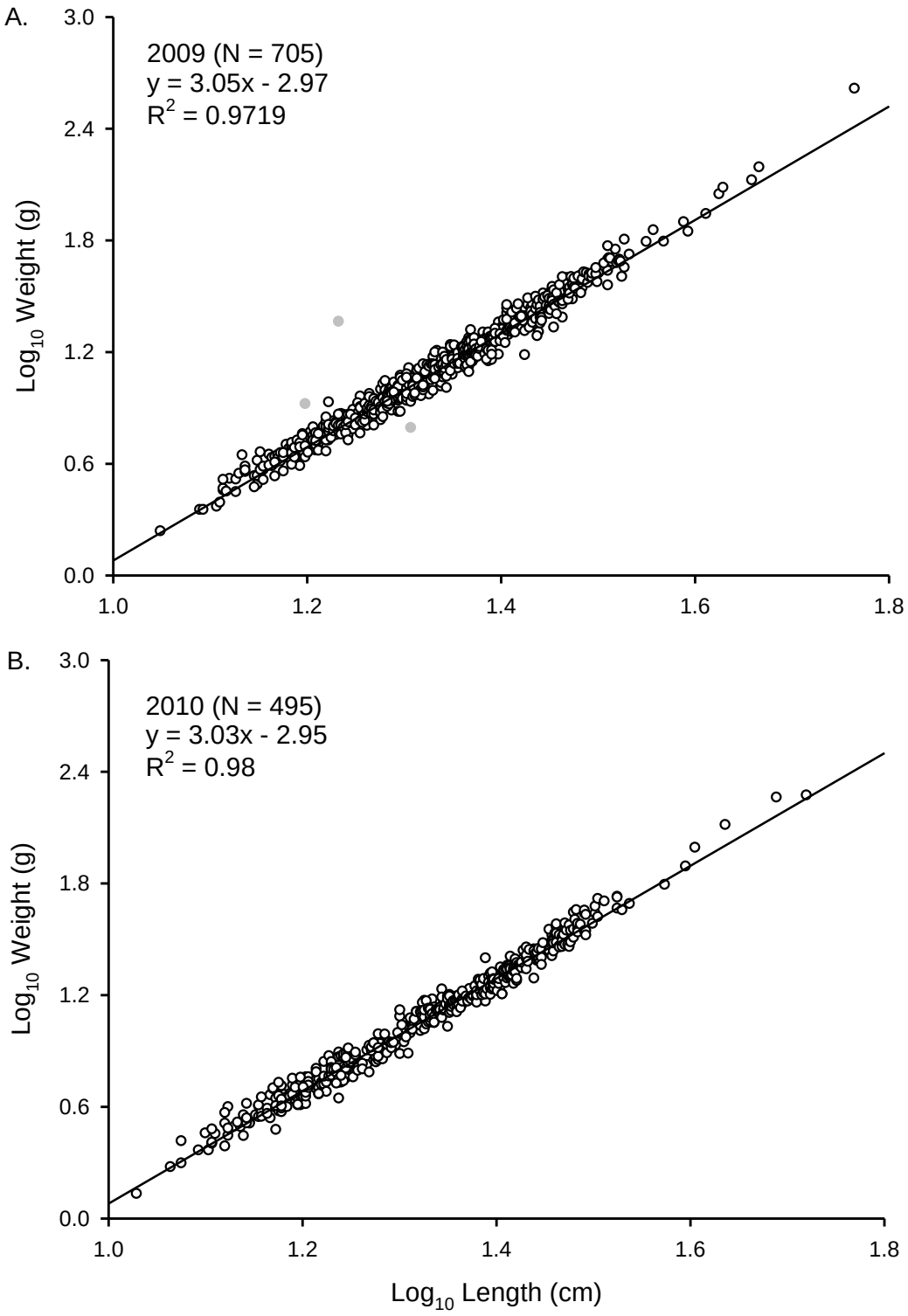

Figure 4.8. Log-transformed weight to length relationship of American eels captured in the Upper Salmon River in a) 2009 and b) 2010. Shaded points indicate outliers that were removed from the ANCOVA analysis and regression line calculation for 2009.

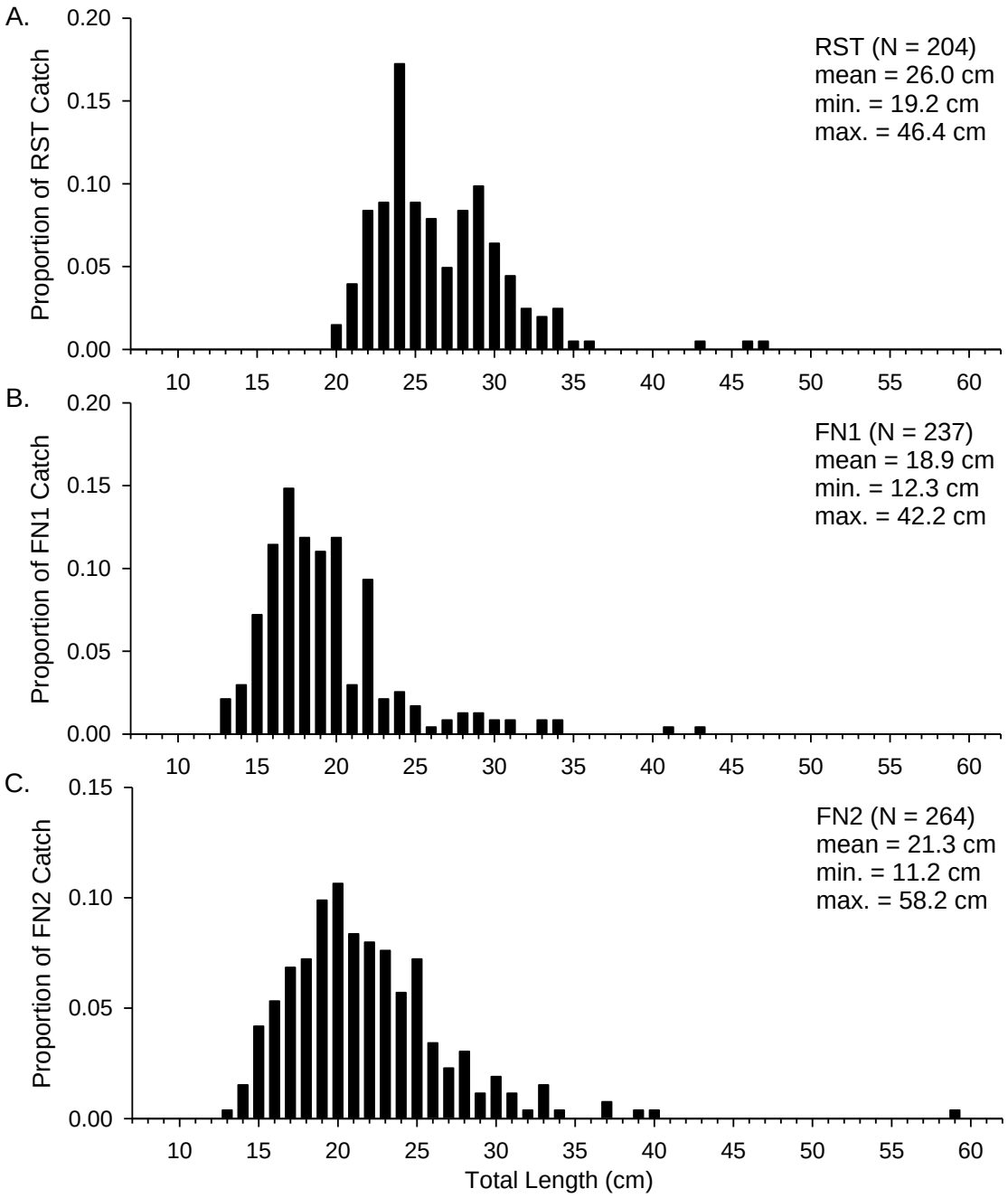

Figure 4.9. Total length distribution of American eels captured at a) the rotary screw trap (RST), b) fyke net 1 (FN1) and c) fyke net 2 (FN2) in the Upper Salmon River in 2009. Each bar represents the proportion of total catch by each trap within a 1 cm length class (i.e., previous 10 mm).

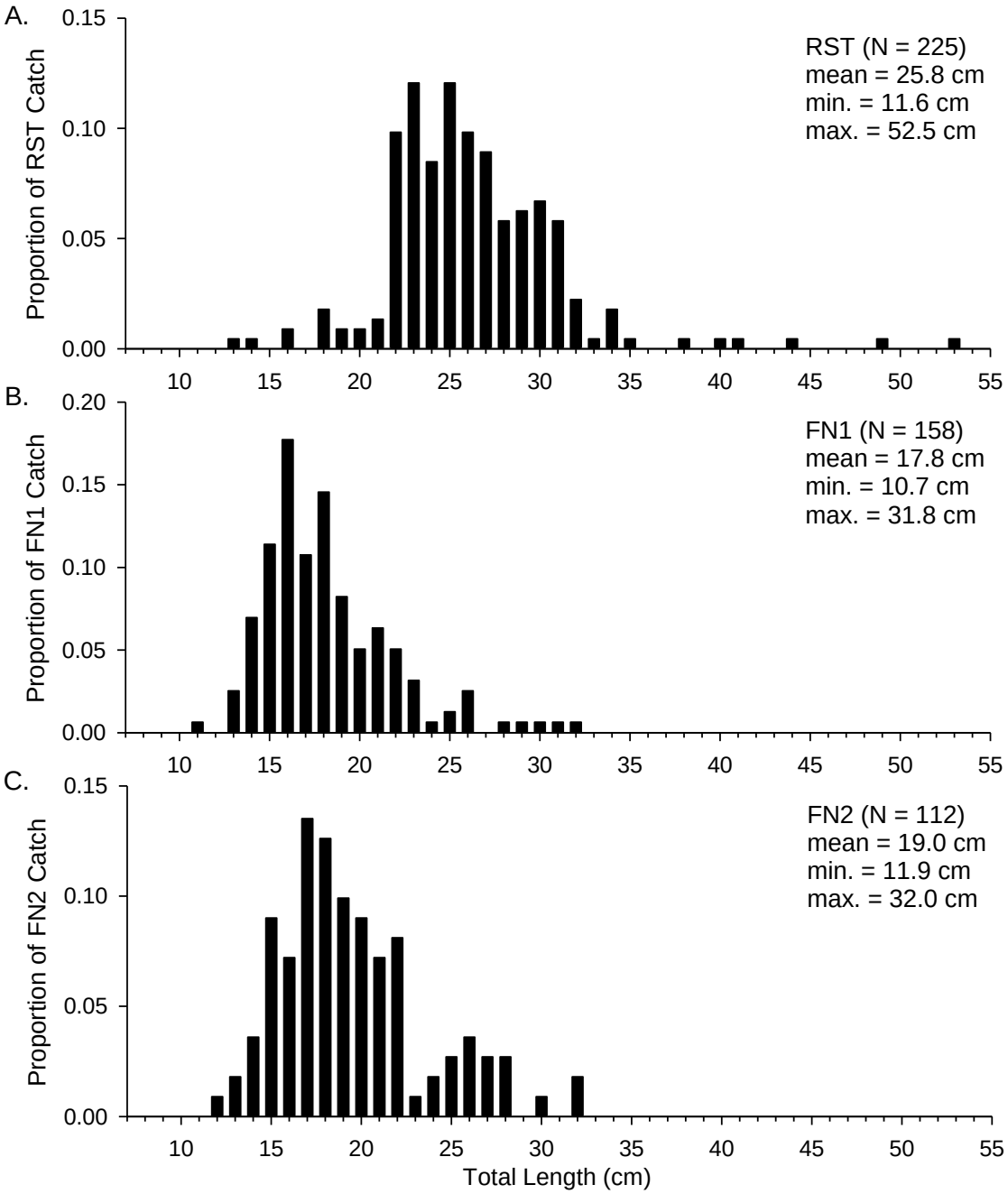

Figure 4.10. Total length distribution of American eels captured at a) the rotary screw trap (RST), b) fyke net 1 (FN1) and c) fyke net 2 (FN2) in the Upper Salmon River in 2010. Each bar represents the proportion of total catch by each trap within a 1 cm length class (i.e., previous 10 mm).

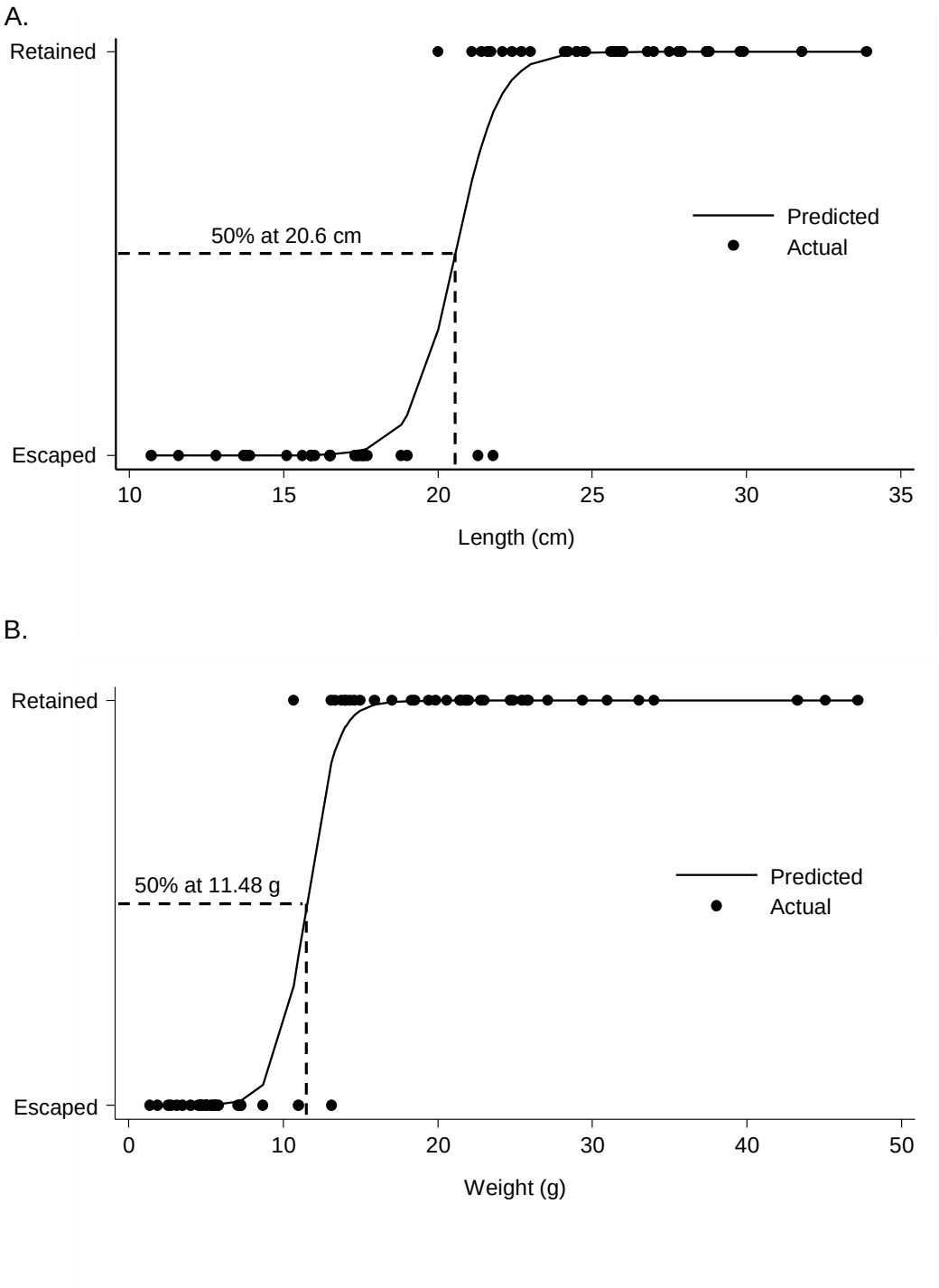

Figure 4.11. Scatter and line plots relating RST retention of American eels after one night in the rotary screw trap holding box (pooled over three trials) with respect to a) length and b) weight of each individual. The solid line indicates predicted values based on logistic regression models. The dashed lines indicate predicted values of the independent variables with 50% retention probability.

5. GENERAL DISCUSSION

5.1. SUMMARY AND CONCLUSIONS

Using two different types of radio telemetry (Chapters 2), this study has shown that American eels migrate seasonally in the Upper Salmon River from saline foraging grounds to freshwater habitat for overwintering as hypothesized by Clément et al. (In Press). Stable isotope analyses showed that the majority of freshwater-captured eels were feeding in saline waters in summer and retain a saline signature throughout the winter, presumably due to a reduced metabolic rate encountered at low temperatures (Walsh et al. 1983). That eels utilize the estuary during summer was confirmed by the manual tracking of PIT tagged eels in the estuary which identified approximately 1/3 of of PIT tagged eels, initially captured in fresh water, within the estuary during low tide. Radio tracking confirmed that a reduced rate of activity occurred during the winter of 2009/2010. Temperature was shown to correlate most with the onset of both spring downstream and fall upstream migrations (Chapter 3). A detailed examination of downstream-migrating American eels enabled an estimate of the number of eels in the Upper Salmon River undertaking downstream migration which was on the order of thousands (Chapter 4). This study has shown that amphidromous migrations are important to American eels in the Upper Salmon River. This study is also a first step in elucidating the ultimate purpose of such migrations.

Although the Upper Salmon River is unusual in estuarine characteristics due to extreme tidal fluctuations, eels migrate in a similar manner in rivers/estuaries under markedly different habitat conditions (Smith and Saunders 1955; Medcof 1969; Jessop 1987; Caron and Raymond 1997). Although eels commonly occupy saline habitats at northern latitudes, winter may present fatal conditions in these areas as a result of subzero temperatures. Seawater at 35 ppt can drop to as low as -1.8 °C before freezing. American eels do not appear to exhibit low-temperature coping mechanisms, such as blood antifreeze proteins (Tomie 2011), which are common to other saltwater fish species; freezing of American eel blood plasma occurs at approximately -0.7 °C (Tomie 2011). Therefore, saline waters approaching or below this temperature threshold may be fatal to overwintering eels and alternative coping mechanisms would be necessary to reduce the risk of freezing.

Two such coping mechanisms appear prevalent based on current knowledge of overwintering eels at high latitudes. Firstly, a historical winter spear fishery has shown that American eels commonly overwinter while burrowed within muddy substrates in brackish estuaries and bays (Tomie 2011). Burrowing in such substrates may be an adaptive mechanism to cope with low temperature stress (Tomie 2011) as soft sediments have been shown to be several degrees warmer than overlying water in winter (Watling 1975), possibly due to reduced flow of water in finer substrates. However, muddy substrates did not appear present in the estuary of the Upper Salmon River which was dominated by a sandy to gravely mixture and such winter burrows, which are usually

indicated by distinct “pock” markings or depressions (Smith and Saunders 1955; Tomie et al. 2013), were not identified during this study. Dynamic winter conditions in the Upper Salmon River due to ice scour (Desplanque and Mossman 1998) could also impact potential eel burrows in the estuary and outer bay, thereby subjecting eels to fatal temperatures, increased predation, or direct physical damage.

The second apparent coping mechanism for low temperature stress in American eels may be direct avoidance of saline habitat in winter. American eels commonly overwinter in freshwater rivers and lakes as well as upwelling springs (Tomie 2011). Because fresh water freezes at a higher temperature (0°C) than saline water and stratified lakes in winter commonly maintain benthic temperatures of 4 °C, overwintering in areas with a degree of freshwater influence eliminates the risk of experiencing fatal temperatures. The search for freshwater habitat may be one factor driving the observed amphidromous migrations between saline foraging habitat and freshwater overwintering habitat in the Upper Salmon River and elsewhere. Areas of the freshwater habitat of the Upper Salmon River in which overwintering eels were found by radio tracking contained boulder substrate. Mud-borrowing would not be possible in these areas but nor would it be required to avoid sub-zero temperatures.

As a panmictic species, hatched eels can be distributed to any locality within its widespread continental range. Therefore, it seems unlikely that eels possess inherent genetic traits which have been selected to dictate behaviours specific to a local area given the wide range of possible environments they encounter. Yet, eels exhibit specific coping

mechanisms or behavioural traits for overwintering in a localized area. Recent research has shown that spatially varying selection may occur over a large geographic area as genetic variation at specific loci was found to correlate significantly with mean surface water temperatures in the area of capture (Gagnaire et al. 2012). However, selection and genetic variation is unlikely to explain local adaptations.

Two possible adaptations which allow American eels to acquire locally adapted behaviours such as amphidromous migration are individual and social learning. Individual learning is a "trial and error" approach whereby an individual fish adapts its behaviour based on the rewards or repercussions of previously exhibited behaviour (Boyd and Richerson 1988). Thus, with respect to overwintering eels, an eel would adjust its overwintering location to a new area if the chosen location presents negative repercussions. However, if overwintering in saline water or dynamic estuaries proves fatal due to low-temperature stress or physical disturbance, reliance on individual learning would be costly to eels at high latitudes and individual learning as an adaptive trait in the larger population would be selected against as a result. The data in the current study does not support individual learning as directed group movements were made upstream at the onset of winter and eels were not identified in the estuary following the upstream migration period, with the exception of a few individuals near the head of salinity.

Social learning is more likely an adaptive trait enabling American eels to exhibit phenotypic plasticity in adapting their behaviour to suit localized conditions. Social

learning is a "learn by observing" behaviour whereby an individual adapts behaviour based on an observation of, or interaction with, other animals (Boyd and Richerson 1988). Social learning has been commonly observed in fish (Brown and Laland 2003). When an individual's behaviour is influenced by a conspecific, this type of social learning is called "conspecific cueing" (Stamps 1987). A naïve eel entering a novel habitat can benefit from following the actions of more knowledgeable individuals without risking the costs associated with individual or "trial and error" learning (Galef 1995). Thus, low temperatures in fall may cue "knowledgeable" eels into moving toward the overwintering habitat in which they spent the previous winter, be it muddy burrows in some estuaries or migration to complete fresh water in others. At the same time, low temperature may also cue social learning in naïve eels wherein they see peers as indicators of favorable overwintering habitat (i.e., conspecific cueing) and follow them to those areas.

Conspecific cueing or attraction as an indicator of preferable habitat may result in the clumping of groups of individuals. This phenomenon has been observed for overwintering eels in a laboratory setting wherein eels clumped together (i.e., burrowed in close vicinity to each other) in overwintering tanks (Tomie 2011). As winter spearing of eels occurs only at sites traditionally known to contain overwintering eels and fishers blindly stab the substrate in search of eels within these areas (Tomie 2011), high densities of eels in localized areas would be required to support such activities. The clumping of

eels in overwintering areas is consistent with social learning via conspecific attraction for identifying suitable overwintering locations.

Social learning is more likely to subject individuals to maladaptive behaviours when environments are highly variable (Boyd and Richerson 1988). Under variable conditions, individual learning is more favorable as the benefits of trial and error learning may outweigh the repercussions of simply following conspecifics (Boyd and Richerson 1988). However, local factors governing the suitability of overwintering habitats at northern latitudes (e.g., dynamics of estuarine habitat, stressful temperatures of saline waters, availability of thermal refugia or cover) are consistent from year to year, and under a constant environment, reliance on social learning results in higher fitness than individual learning (Boyd and Richerson 1988).

Reliance on social learning in identifying suitable overwintering habitat may subject eels to high risk upon introduction of sudden environmental changes in normally consistent environments. For example, sharp changes to temperature regimes, such as those caused by global climate change, could alter the location of the most favorable overwintering habitat for American eels in a local area. However, with continued reliance on conspecific cues, eels may continue to overwinter in habitats that have become unsuitable as a result (e.g., increased temperatures resulting in increased metabolic rate and depletion of fat stores throughout the overwintering period). A small subset of some eels in localized areas may exhibit individual learning to identify novel overwintering locations. However, transfer of this knowledge to the greater population through

selection (i.e., higher rate of survival for a few eels in novel overwintering areas) in conjunction with social learning (i.e., exponential growth in the number of eels overwintering in preferable areas through conspecific cuing) may require many winters. Therefore, sudden environmental changes will have a greater impact on localized groups that can't quickly identify suitable overwintering habitat. The inability to identify and utilize novel overwintering habitats at a sufficient rate would also subject eels to greater risk with respect to the introduction of migration barriers such as dams. For example, should a dam be introduced into the Upper Salmon River in summer while eels are foraging in the estuary, eels may not survive the winter by identifying novel and suitable overwintering habitat once inhibited from reaching the overwintering habitat utilized in the previous winter.

5.2. FUTURE RESEARCH

Future research that focuses on overwintering habitat selection by American eels will aid managers in pinpointing and preserving critical overwintering habitats in the wild and understanding why specific micro-habitats are chosen over others. Such behavioural studies will also help determine why American eels undertake seasonal amphidromous migrations in some areas.

Holding tank experiments in which each tank is divided to provide two conditions between which eels can move freely would allow testing of various hypotheses. Tests should be initiated in summer, allowing eels to acclimatize to laboratory conditions, and

continued through fall and the onset of the overwintering period. Firstly, providing fresh water or low-salinity vs. high-salinity conditions will test the prediction that eels migrate to fresh water, or areas of low salinity, to reduce the risks associated with low temperature stress. As burrowing in mud may reduce the chances of freshwater habitat selection, no burrowing substrate should be supplied in these experiments; cover can be presented in the form of plastic tubes in both the saline and low-saline tanks.

In a complementary experiment, to test the hypothesis that eels in saline water burrow in mud in order to mitigate risks associated with sub-zero temperatures, mud should be placed in the bottom of tanks containing either fresh water or saline water and maintained above 0°C (e.g., by use of an underlying heating element) to determine if eels overwintering in saline water are more likely to burrow in mud than those overwintering in fresh water. Alternative cover to mud burrows (e.g., plastic tubes) should also be provided in both tanks to alleviate the effects of burrowing as a need for cover as opposed to geothermal refugia.

The above test could also incorporate a test of whether burrowing eels choose to overwinter together (clump), as would be expected if social learning were involved, or apart. The holding tanks would need to be fairly large relative to the size of the eels and multiple eels would be introduced simultaneously. If eels are unevenly distributed within tanks that present identical overwintering conditions on both sides, this would support the hypothesis that eels chose habitat based on social learning and clumping into one side of

a tank may be a result of conspecifics selecting an overwintering area based on the selection of its peers.

5.3. MANAGEMENT IMPLICATIONS

This study has shown that American eels in the Upper Salmon River migrate between saline summer foraging and freshwater overwintering habitat. If American eels undertake amphidromous migrations as a requirement for survival, managers must ensure eels have unimpeded access to target habitats where, and when, these migrations occur. However, to do this requires knowing the sites in which eels make these seasonal movements rather than staying in the estuary year-round and at present, this information exists for few sites.

Prior to this study, the presence of amphidromous migrating American eels in the Upper Salmon River was unproven but suspected based on rotary screw trap records indicating downstream migrations occurring regularly in spring. Similar records of spring-migrating American eels have been reported from rotary screw trap programs throughout eastern Canada (Caron and Gauthier 2003; Chaput and Jones 2004; Caron et al. 2005; Flanagan et al. 2006; Cairns et al. 2007; Clément et al. (In Press); Thibault et al. 2007b; Breau et al. 2010). Further research is needed to determine the geographic extent in which American eels that undertake seasonal migrations between saline and freshwater habitats. The simplest method to determine the extent of amphidromous-migrating eels would be to complete electrofishing within the overwintering period upstream of the head

of salinity in numerous rivers over a large geographic extent. Electrofishing should be completed in early to mid-November when rivers are generally free of ice and eels have moved to their overwintering grounds. Fin tissue of collected eels could be analyzed for stable isotope analysis to determine if eels collected in fresh water contain saline isotopic signatures, suggesting foraging in saline habitat the previous season. However, as electrofishing has been shown to be harmful to American eels (Reynolds and Holliman 2004), particularly those overwintering (Chapter 3), fyke nets may be a more appropriate sampling method. Fyke nets could be positioned, as in the current study, above the head of salinity and upstream-directed to target downstream-migrating eels. Nets could be installed for shorter periods (i.e., 1-2 nights) to collect a small sample of eels (i.e., 10 eels) before removing nets for installation in other rivers throughout the migration period. In addition to collecting isotopic information, use of fyke nets would provide more powerful evidence of amphidromous migrations as it would indicate that eels were physically migrating in spring.

Both of the suggested studies will aid managers in identifying important habitats to American eels at northern latitudes. Upon identifying such habitats, ensuring that the quality of, and access to, these areas is maintained will contribute to the overall conservation of the American eel in the northern extent of their range.

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APPENDIX 1. RECAPTURE MATRICES

Table A-1: Recapture matrix for the mark-recapture experiment using PIT tagged yellow-stage American eels >20 cm during downstream migration in 2009. Tagged eels were released 600 m upstream of the capture location and recaptured by the RST and/or one of two fyke nets. n = number of PIT tagged eels released

Release Date	n	Recapture																																																	
		May																			June																														July		
		13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3
13-May	4	-																																																			
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15-May	20			-																	1																																
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25-May	36													-							2												2																				
26-May	2														-																																						
27-May	3															-																																					
28-May	1																-																																				
29-May	2																	-																																			
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31-May																				-																																	
01-Jun	62																				-																																
02-Jun	6																					-																															
03-Jun	4																						-																														
04-Jun	5																							-																													
05-Jun	4																								-																												
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24-Jun	2																																											-									
25-Jun	11																																												-								
26-Jun	4																																													-							
27-Jun																																															-						
28-Jun																																																-					
29-Jun																																																	-				
30-Jun																																																		-			
01-Jul																																																			-		
02-Jul	1																																																			-	
03-Jul	3																																																				-
Total	**383**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**5**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**2**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

Table A-2: Recapture matrix for the mark-recapture experiment using PIT tagged yellow-stage American eels >20 cm during downstream migration in 2010. Tagged eels were released 600 m upstream of the capture location and recaptured by the RST and/or one of two fyke nets

Release Date	Number Released	Recapture																																								Total
		April		May																																June						
		29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	
29-Apr	0	-																																							0
30-Apr	0		-																																						0
01-May	0			-																																				0
02-May	0				-																																			0
03-May	0					-																																		0
04-May	29						-				2																														2
05-May	8							-			1																														1
06-May	7								-									1				1																			2
07-May	0									-																															0
08-May	5										-							1																							1
09-May	0											-																													0
10-May	0												-																												0
11-May	0													-																											0
12-May	0														-																										0
13-May	1															-																									0
14-May	0																-																								0
15-May	0																	-																							0
16-May	17																		-			2																			2
17-May	11																			-																					0
18-May	6																				-																				0
19-May	15																					-			1																1
20-May	4																						-																		0
21-May	9																							-																	0
22-May	0																								-																0
23-May	0																									-															0
24-May	1																										-														0
25-May	0																											-													0
26-May	5																												-											1	1
27-May	0																													-											0
28-May	0																														-										0
29-May	0																															-									0
30-May	0																																-								0
31-May	0																																	-							0
01-Jun	0																																		-						0
02-Jun	0																																			-					0
03-Jun	0																																				-				0
04-Jun	0																																					-			0
05-Jun	0																																						-		0
06-Jun	0																																							-	0
Total	118	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	10

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