

THE ESTUARINE AND EARLY MARINE SURVIVAL OF ATLANTIC SALMON:
ESTIMATION, CORRELATES AND ECOLOGICAL SIGNIFICANCE

by

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"Never doubt that a small group of thoughtful,
committed citizens can change the world.
Indeed, it's the only thing that ever has".

Margaret Meade

**For all the unwaivering souls who,
in the face of relentless onslaught and looming crisis,
continue to fight for wild fishes and the places they live.**

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ABSTRACT

This thesis focuses on the estuarine, coastal and marine mortality of Atlantic salmon. The overall objective is to better understand the factors affecting the survival of Atlantic salmon during their early marine phase. To meet this objective, we first review trends in marine survival, and examine theoretical and empirical evidence to identify; (a) potentially important mortality sources, and (b) the timing of high mortality. It is clear that widespread shifts in the marine survival of salmon have occurred, however the timing, magnitude and effect of survival shifts is variable. Likely mortality mechanisms are similarly variable. This review highlights predation during the early marine phase as important for North American salmon; thus granting focus to the remaining research chapters.

We next estimate the survival of postsmolts in selected estuaries and coastal habitats using acoustic telemetry. Simultaneously, we incorporate methods to address the major limitations to estimating survival using acoustic telemetry, including the use of mark-recapture modelling to address the effect of receiver detection performance, and a novel cluster-analysis modelling approach that attempts to quantify the complicating effects of predation. Our findings suggest that the early marine survival of Atlantic salmon, similar to marine mortality as a whole, is highly variable. Cumulative survival through the river, inner estuary, outer estuary and bay habitats ranged from 39.4% to 73.5% in Nova Scotia's Southern Upland, whereas survival past the outer estuaries of inner Bay of Fundy rivers ranged from 24.3-54.0%. Survival rates followed two patterns: (1) constant rates of survival independent of habitat or (2) low survival most frequently associated with inner estuary habitats. We also examine the potential mortality mechanisms related to predation by examining patterns in the estuarine mortality of acoustically tagged salmon juveniles, using insights from mortality covariates, and the relationship between migratory behaviour and survival. Avian predation appears to be the dominant mortality vector in some estuaries of Nova Scotia's Southern Upland, with the sudden disappearance of most (75–100%) smolts and post-smolts; which we interpret as evidence of avian predation along with evidence of size-selective survival. Alternatively, predatory striped bass appear to be a major source of mortality for some inner Bay of Fundy salmon populations, with evidence of a minimum of 7.3-27.3% of all tagged smolts being consumed by striped bass, based on migratory movement patterns.

The survival estimates reported in this thesis permit the division of the marine phase into two periods; an early period encompassing estuarine and coastal habitats (< 1 month), and the remaining time at sea. By comparing estimated survival during these two periods, it appears that estuarine survival cannot be solely responsible for observations of reduced marine survival since approx. 1990. The highest marine mortality must occur outside of estuaries and early coastal habitats. However, efforts directed at reducing estuarine and coastal mortality may be valuable for conservation planning, and may help reduce the risk of extirpation and, in some cases, may lead to viable populations.

LIST OF ABBREVIATIONS USED

1SW	One sea winter
2SW	Two sea winter
AIC	Akaike information criterion
AIC_c	Second-order Akaike information criterion
\hat{c}	Quasi-likelihood over-dispersion parameter
CI	Confidence interval
CJS	Cormack-Jolly-Seber
EBFM	Ecosystem-based fisheries management
FW	Freshwater
GLM	Generalized linear model
GoF	Goodness-of-fit
HoT	Head of tide
HSD	(Tukey's) Honest significant difference
iBoF	Inner Bay of Fundy
IE	Inner estuary
L_F	Fork length
OE	Outer estuary
P_{DR}	Probability of being detected at river mouth and re-assigned as within a striped bass
P_{DS}	Probability of being detected at river mouth and assigned as a salmon smolt

P_S	Probability of surviving
P_U	Probability of being undetected
P_{UR}	Probability of being undetected at river mouth and re-assigned as within a striped bass
P_{US}	Probability of being undetected at river mouth and assigned as a salmon smolt
QAIC	Quasi-Likelihood Akaike Information Criterion
S_{early}	Survival within estuarine and coastal habitats as post-smolts
S_{later}	Remainng marine survival after S _{early} .
SOR	Standardized overall residency
SU	Southern Upland
TMR	Tag-to-body-mass ratio
β	Beta parameter

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CHAPTER 1: INTRODUCTION

Atlantic salmon, *Salmo salar* L. are valued for a number of reasons: as an iconic ecosystem component, for their recreational and commercial value, and by First Nations for ceremonial and food purposes (Dunfield 1985, Beland and Bielak 2002). Despite this, most Atlantic salmon populations have declined throughout the last century due to a number of factors including freshwater habitat degradation and fragmentation, over-exploitation and altered ecosystems (WWF 2001, Potter et al. 2003). Most strikingly, these declines have occurred at an accelerated rate over the last two decades (Mills 2000, Hawkins 2000), particularly for populations at the southern limit of the species' distribution (Parrish et al. 1998, COSEWIC 2011).

Atlantic salmon are predominantly an anadromous species (although non-anadromous forms exist; *see* Power 1958, Havey and Warner 1970, MacCrimmon and Gots 1979), spending between one to eight years in freshwater (Metcalf and Thorpe 1990, Gibson 1993) prior to entering the sea as smolts. Salmon spend one to three winters in the ocean before returning as mature adults to spawn for the first time (Porter et al. 1986, Klemetsen et al. 2003, Webb et al. 2007). While at sea, salmon are considered postsmolt until the end of their first winter at sea, after which they are termed one sea-winter salmon (or two/three sea winter salmon as appropriate; Allan and Ritter 1987). Atlantic salmon are also iteroparous, and have been recorded spawning as many as seven times (ICES 2004) typically spending one or two additional winters at sea between spawning events (Jonsson et al. 1991).

By comparing trends in salmon survival during these two major phases of the Atlantic salmon's life history, the timing of significant population declines can be attributed to either the freshwater or marine environment. Freshwater productivity (i.e. egg-to-smolt survival) is highly variable among sites and years (Chaput et al. 1998), however, within-population means have remained fairly constant over the last two-three decades in many populations (Baglinière et al. 2005, Gibson and Claytor 2012). By

contrast, survival from smolt to returning spawner (adult) has declined dramatically since approximately 1990 (Jonsson and Jonsson 2004, Chaput et al. 2005, Chaput 2012). Due to the fact that this phase (smolt-to-spawner) occurs primarily (ca. 70-95%) in estuarine and marine environments, the problem most-likely occurs within these habitats. Thus, the widespread and rapid declines of salmon that have occurred in Europe and North America appear to be the result of reduced survival at sea (Hutchinson and Mills 2000, Hawkins 2000, Gibson et al. 2009; 2011). This thesis focuses on the estuarine and marine survival of Atlantic salmon.

1.1 OBJECTIVES AND THESIS OVERVIEW

Conservation planning requires the identification of factors that limit population recovery. Identifying the cause(s) of widespread survival shifts in the marine survival of salmon is fraught with challenges including; an incomplete understanding of the marine ecology of Atlantic salmon, the existence of only a coarse understanding of their marine migration routes, limited population and cohort-specific time series of marine return rates (e.g. ICES 2013), and a scarcity of estimates of marine survival at time scales less than the full marine cycle from smolt to returning adult.

The overall goal of this thesis is to better understand the factors affecting the survival of Atlantic salmon during the early marine phase of their life history. To attain this goal, the research outlined in this thesis has the following four primary objectives:

1. Identify potential mechanisms responsible for recent (i.e. since 1990) poor marine survival and identify when important periods during the marine phase of salmon are likely to occur, by reviewing the available literature .
2. Estimate the survival of postsmolts in selected estuaries and coastal habitats using acoustic telemetry.
3. Test the potential sources of mortality identified in the literature review by examining patterns in mortality of acoustically tagged salmon juveniles, using

insights from mortality covariates and the relationship between migratory behaviour and survival.

4. Incorporate methods to address the major limitations to estimating survival using acoustic telemetry, including the use of mark-recapture modelling to address the effect of receiver detection performance and a novel modelling approach that attempts to quantify the complicating effects of predation; thus improving future estimates of marine survival for Atlantic salmon.

This thesis consists of six chapters including an introduction, general conclusion and four research chapters. The first research chapter is a literature review and synthesis while the other three research chapters describe field-based and modelling research. Some of these chapters simultaneously address more than one research objective (Table 1.1).

Chapter two reviews existing literature on the marine survival and ecology of Atlantic salmon; emphasizing the potential associations between ecosystem regime shift (e.g. Beaugrand and Reid 2003; 2012, Bundy 2005, Frank et al. 2005) and marine survival. We identify two major findings that focus all subsequent research efforts. First, we highlight the potential role of survival during the very early portion of marine residency for North American populations, a period that includes estuaries and coastal habitats. Second, we provide evidence for the potentially dominant role played by predation during this period. Guided by these two major findings, chapters 3-5 report efforts to 1) estimate estuarine and coastal survival rates using acoustic telemetry, 2) identify potential causes of mortality (mortality vectors), and 3) address the limitations of using acoustic telemetry to estimate survival rates.

In an effort to highlight the variability in the estuarine survival of Atlantic salmon, we examine populations from four rivers in Nova Scotia's Southern Upland (SU) region and two rivers from the inner Bay of Fundy (iBoF) region. These two distinct designatable units (meta-populations) have been evaluated as endangered (COSEWIC 2011), with the latter formally protected under Canada's Species at Risk Act (DFO 2008).

Freshwater, estuarine and coastal habitats differ between these two regions, as do predator fields, thus survival rates and mortality vectors likely also vary between the two regions. Further, significant life history variability (e.g. marine maturation rates) exists among rivers within each region, therefore survival rates may also vary at a population-scale. As a generalization, estuaries in the SU are subject to small tidal range (e.g. < 2m) and contain water of low suspended particulate concentrations. In contrast, estuaries in the iBoF are subject to extreme tides (10-16m), including tidal bores (Greenberg 1984, Rulifson and Tull 1999) and contain water with high levels of suspended sediment (Amos and Alfoldi 1979). Marine return rates for these two regions currently differ by approximately an order of magnitude. The role of estuarine and early marine survival may be dramatically different between these two areas.

These populations also differ in the expected vectors of mortality, and thus each provides unique opportunities to apply novel approaches to identifying mortality vectors and to also address the limitations of using acoustic telemetry to estimate survival. In the SU, predation by avian predators is considered an important mortality vector for salmon smolts / postsmolts (Milton et al. 1995) whereas the abundance of piscivorous fishes in SU estuaries is considered minimal and thus they are not likely an important mortality vector. Smolts from this region also experience acidic freshwater conditions (Watt et al. 1983, Lacroix 1987, Lacroix and Korman 1996, Watt et al. 2000) which can reduce their ability to adjust to the marine environment (Staurnes et al. 1996, Magee et al. 2003, Monette et al. 2008) and consequently, elevate their risk of predation (Järvi 1989, Handeland et al. 1996, McCormick et al. 1998) and decrease marine survival (Kroglund and Finstad 2003, Kroglund et al. 2007). Alternatively, avian predators in iBoF estuaries are not widely considered a major source of predation on salmon smolts, presumably due to the opacity of the water. However, striped bass, *Morone saxalitis* are a known predator of salmon smolts (Blackwell and Jaunes 1998, Beland et al. 2001) and occur at high density in several iBoF estuaries. Life histories vary at a river-scale or tributary scale, with populations characterized by predominantly 1SW or 2SW returning adults present in both regions.

Chapter three details the use of acoustic telemetry to estimate the estuarine and coastal survival of smolts from the SU. With the expectation that avian predators may remove a portion of the tagged smolts from the water, we combine passive and rigorous active telemetry techniques to determine the ultimate fate of tagged smolts and estimate the rate of avian predation, where tags that “disappeared” from the study site were assumed to have been consumed by avian predators.

The results identified two patterns: constant rates of survival independent of habitat when salmon migrated directly to the ocean at a constant rate, or variable survival that was lowest within inner estuary habitats associated with frequent migration reversals (back-and-forth movements). These two patterns were suggestive of a relationship between migratory behaviour and survival. Further, it was apparent that some fish migrated past receivers without being detected. Poor detection efficiency of acoustic receivers confounds survival estimates generated from acoustic telemetry (Voegeli and Pincock 1996, Melnychuk 2012). Thus, in an effort to evaluate the utility of several survival covariates and estimate the impact of detection efficiency on survival estimates, we fit Cormack-Jolly-Seber mark-recapture models (Cormack 1964, Jolly 1965, Seber 1965) to the detection histories of the acoustically tagged smolts. We also formally tested the relationship between migratory behaviour and survival. These latter results are presented in **chapter four**.

Again using acoustic telemetry and mark-recapture models, we estimate estuarine and coastal survival for two iBoF salmon populations in **chapter five**. However, the complicating effect of predation on survival estimates was a concern in these iBoF rivers due to the high densities of predatory striped bass, particularly during their spawning times which overlap both spatially and temporally with smolt migrations. Striped bass form large aggregations during the spawning period (COSEWIC 2012). When predation on tagged smolts occurs, the transmitter can continue to be detected while in the predator’s gastro-intestinal track (Beland et al. 2001). Detections of such tags can give false impressions that the tagged smolt remains alive when, in fact, it has been preyed upon. Therefore, we developed an approach to estimating survival after accounting for

the complicating effect of predation, using cluster analysis to identify common migratory patterns between salmon smolts and striped bass.

In the conclusion of this thesis (**chapter six**), the population-level significance of the estimated early marine mortality is discussed, specifically whether these mortality levels could account for the observed shifts in marine return rates and whether focusing conservation/mitigation efforts is likely to result in viable Atlantic salmon populations. Further, the finding of predation as an important mortality vector in estuaries and coastal areas is discussed along with potential options for conservation planning. Finally, the implications of addressing detection efficiency and predation when estimating survival using acoustic telemetry are discussed, and considerations to improve the future use of telemetry for estimating survival is also provided.

Much of the research presented in this thesis was a collaborative effort between I, Edmund A. Halfyard, my thesis co-supervisors; Dr. Fred Whoriskey and Dr. Daniel Ruzzante, members of my supervisory committee; Dr. Jamie Gibson (Fisheries and Oceans Canada, Dartmouth, NS), external advisors; Dr. Mike Stokesbury (Acadia University, Wolfville, NS) and several other co-authors. Accordingly, the pronoun “we” is used extensively throughout this thesis, and reflects the contributions of my co-authors.

1.2 PUBLICATIONS ARISING FROM THIS THESIS

At the time of thesis submission, chapters 3 and 4 have been published, and chapter 5 submitted as follows, respectively;

- (1) Halfyard, E.A., Gibson, A.J.F., Ruzzante, D.E., Stokesbury, M.J.W., and Whoriskey, F.G. 2012. Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology* **81**: 1626–1645.
doi:10.1111/j.1095-8649.2012.03419.x
- (2) Halfyard, E.A., Gibson, A.J.F., Stokesbury, M.J.W., Ruzzante, D.E. and Whoriskey, F.G. 2013. Correlates of estuarine survival of Atlantic salmon

postsmolts from the Southern Upland, Nova Scotia, Canada. Can. J. Fish. Aquat. Sci. **70**: 452–460. doi: dx.doi.org/10.1139/cjfas-2012-0287.

- (3) Gibson, A.J.F., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J.W. and Redden, A.M. Submitted. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Canadian Journal of Fisheries and Aquatic Sciences.

Chapter two will be formatted for publication. I will be the lead author while Daniel. E. Ruzzante and Fred. G. Whoriskey will be co-authors.

Table 1.1- Cross-cutting of objectives and research projects.

Objective	<i>Research Chapter</i>			
	Chapter 2	Chapter 3	Chapter 4	Chapter 5
Narrow research focus	•			
Estimate survival		•	•	•
Identify mortality vectors		•	•	•
Address limitations of acoustic telemetry				
Detection efficiency			•	•
Effect of predation				•

Note: A dot denotes which objectives are addressed in each research project.

CHAPTER 2: SHIFTS HAPPEN: A REVIEW OF THE IMPACT OF ECOSYSTEM REGIME SHIFT ON ATLANTIC SALMON

2.1. ABSTRACT

Atlantic salmon populations have recently declined across much of their distribution and these declines are largely the result of poor marine survival. There is emerging evidence that the marine survival of salmon has declined significantly. This decline has been abrupt, appears to be persistent and several studies have suggested a link to the widespread ecosystem regime shift that has occurred across much of the North Atlantic Ocean. The current evaluation of mechanisms linking changes in salmon survival to widespread ocean regime shift has, however, been largely focused on trophic levels below Atlantic salmon, thus neglecting the potential role of predation.

Here, we review evidence of shifts in the marine survival of virgin and repeat-spawning Atlantic salmon and discuss the limitations of these data. Further, we also review theoretical and empirical evidence that both prey availability and predation may be important drivers of reduced marine survival of Atlantic salmon, and highlight the spatial variability of these drivers.

Recent marine return rates declined in nearly all monitored populations and life stages, however, there are exceptions involving at least two populations of repeat spawning salmon which experienced a shift to increased survival. Survival shifts in virgin salmon were concurrent with widespread ecosystem reorganization across the North Atlantic Ocean, and shifts in the marine survival of repeat spawning salmon occurred as the abundance of many species fluctuated. The abundance of European Atlantic salmon correlates with the abundance of prey species, and given a positive growth-survival relationship, this relationship appears to represent a “bottom-up” pathway affecting Atlantic salmon survival. Conversely, despite correlations between North American salmon abundance and prey species, the lack of a growth-survival relationship in North America suggests that other factors, most likely predation, have driven survival shifts. Predation pressure in North America has increased as a result of elevated predator abundance as well as a functional response of some predators to changing conditions that shift focus toward Atlantic salmon.

In this review, we outline the diversity of factors potentially affecting the marine survival of Atlantic salmon and highlight the need for multiple approaches to conservation. Further, the presence of survival shifts affecting repeat spawning Atlantic salmon suggests that mitigation options focusing on these older fish may provide, in some populations, increased overall conservation value relative to virgin spawners.

2.2. INTRODUCTION

Most Atlantic salmon, *Salmo salar* L., populations have declined throughout the last century due to a number of factors including freshwater habitat degradation and fragmentation, as well as over-exploitation (WWF 2001, Potter et al. 2003), despite their significant ecological, recreational, commercial and ceremonial value. Most strikingly, these declines have occurred recently at an accelerated rate since approximately 1990 (Mills 2000, Hawkins 2000), particularly for populations at the southern limit of the species' distribution (Parrish et al. 1998, COSEWIC 2011).

Declines of European and North American salmon appear to be the result of reduced smolt-to-spawner survival (Hutchinson and Mills 2000, Hawkins 2000, Gibson et al. 2009; 2011) while freshwater egg-to-smolt survival has remained relatively unchanged (e.g. Baglinière et al. 2005, Gibson and Claytor 2012). Because the smolt-to-spawner phase occurs primarily (ca. 70-95%) in estuarine and marine environments, the problem most likely occurs within these habitats. The proper identification of the causes of poor marine survival is hampered by our poor knowledge of the ecological niche of salmon in complex marine food webs, the potential diversity of causal mechanisms acting on the species multiple life stages that occupy the marine environment, ontogenetic diet shifts and opportunistic feeding by Atlantic salmon that make prey-salmon relationships unclear, the highly migratory nature of salmon, and an incomplete understanding of the salmon's marine migrations. Finally, as a result of trophic cascades and complex trophic interactions it is often difficult to disentangle the effects of bottom-up climatic forcing and top-down predation as factors affecting Atlantic salmon at sea.

The recent rapid reorganization of the ocean ecosystem of the north Atlantic has altered energy-flow pathways resulting in changes in the abundance, diversity and distribution of marine species (Beaugrand and Reid 2003, Bundy 2005, Frank et al. 2005). As a result, several species of marine fish have exhibited sharp declines in abundance, recruitment or survival (Bundy 2005, Beaugrand and Kirby 2010). Even as an anadromous species at low biomass, Atlantic salmon in the ocean are likely to be similarly affected. Given these widespread and abrupt changes, rapid declines in the abundance or marine survival of Atlantic salmon across many river systems may signify a common causal mechanism, or at least a relationship, with ecosystem regime shift (Beaugrand and Reid 2003;2012, Mills et al. 2013).

Here, we review the evidence that Atlantic salmon survival has changed in an abrupt, persistent and substantial manner indicative of a shift. The available evidence of widespread ecosystem regime shift in the ocean is reviewed and the potential links between ecosystem regime shift and salmon survival is explored. Potential mechanisms linking ecosystem regime shift to Atlantic salmon survival in the ocean are assessed, focusing on the direct effects of climate and the indirect effect effects of reorganized marine ecosystems and altered trophic interactions.

2.3. EVIDENCE OF SHIFTS IN THE MARINE SURVIVAL OF ATLANTIC SALMON

Atlantic salmon occupy the marine environment from the period from when they leave their natal rivers as postsmolt until they return as virgin spawners, generally spending one (1SW) or two winters at sea (2SW) prior to maturing for the first time (virgin spawners). Additionally, salmon occupy the ocean during a second important phase of their life cycle; as post-spawn adults reconditioning at sea so that they may spawn again. Adults that survive their first spawning event return to sea to feed heavily, reconditioning body energy reserves for another chance to spawn. Atlantic salmon have been noted to spawn up to six (Ducharme 1969) or seven (ICES 2004) times over their lifespan. These repeat spawners (a.k.a. salmon kelts, slinks or black salmon) may return

to the river after just a few months at sea (consecutive repeat spawner) or after spending one or more additional winter at sea (alternate repeat spawner). In this section we review the evidence suggesting that the marine survival of both virgin and repeat spawning Atlantic salmon has declined substantially and abruptly, rather than in a gradual way, since the 1980s (Fig. 2.1). This will be followed by a discussion of the sources of uncertainty in this evidence.

An initial abrupt and sustained drop in the nominal commercial catch of salmon occurred in the northeast Atlantic Ocean in 1988 (Beaugrand and Reid 2003) and a second decline was identified in 1996/1997 (Beaugrand and Reid 2012). In 1988 the decline involved both maturing and non-maturing salmon while in 1996/1997 only salmon maturing as 1SW exhibited a decline (Beaugrand and Reid 2012). Atlantic salmon in the northwest Atlantic Ocean also appear to have experienced abrupt changes in marine survival as revealed by a region-specific analyses of prefishery abundance (PFA) and marine productivity (prefishery abundance relative to the index of spawning escapement, Mills et al 2013, Fig. 2.1). First, four of six regions analysed (the four southernmost regions, i.e., all but Newfoundland and Labrador) showed sharp declines in abundance and marine productivity beginning around 1990. By contrast, PFA of Newfoundland and Labrador populations exhibited a more gradual decline and an abrupt shift in marine productivity did not occur here until 1998. These findings corroborate those of Chaput et al. (2005) who modelled time series of marine productivity and demonstrated overwhelming evidence of a negative shift around 1990. A 1996/1997 shift was not evident in the analysis by Chaput et al. (2005), but could have been concealed in some regions as their analysis aggregated data for all six North American regions.

There is also emerging evidence that the survival of repeat-spawner salmon has changed in an abrupt, persistent and substantial manner though sometimes this shift led to increased survival rather than reduced survival (Fig. 2.2). Niemelä et al. (2006) reported a 30 year time series of repeat spawner survival from the River Teno, in northern Scandinavia where there was a dramatic rise in the return rates of repeat spawning salmon (particularly females) beginning in the late-1990s. Likewise, the survival of

repeat spawners in the Miramichi River, New Brunswick, Canada may have recently increased. Chaput and Benoît (2012) provided evidence that return rates of consecutive repeat spawners have increased dramatically in the mid-1990s while return rates of alternate repeat spawners have remained unchanged.

By contrast, the survival of repeat spawners from the Lahave River, Nova Scotia (Canada) declined abruptly in the early-1990s for all repeat spawners during their first year post-spawn but has remained relatively unchanged during their second year post-spawn (Hubley and Gibson 2011). Repeat spawners also constituted a declining portion of the population in the St. John River, New Brunswick (Canada, Chaput and Jones 2006), however, these data do not represent survival and thus the presence of a shift is unclear.

2.3.1. SOURCES OF UNCERTAINTY

Direct measurement of the marine survival of Atlantic salmon is difficult and though several proxies are available, all have limitations and none provide a direct estimate of survival. The detection of shifts in the marine survival of salmon can thus be challenging and may be influenced by the selection of marine survival proxies as well as by the spatial scale of the analyses.

To date, researchers have focused on nominal salmon commercial catch, salmon abundance (e.g. prefishery abundance, PFA), or marine productivity (e.g. PFA relative to lagged spawner escapement) with the assumption that these metrics are largely driven by marine survival. However, PFA estimates and nominal catch data fail to account for lagged egg deposition (i.e. previous spawner abundance) and freshwater survival. Given the density dependent relationship between spawner abundance and subsequent smolt production (e.g. Jonsson et al. 1998, Gibson 2006), isolating the marine environment and disentangling freshwater and marine effects is important when assessing marine mortality in salmon. In practice, this is, however, difficult to accomplish (Chaput 2012). Marine productivity (e.g. Chaput et al. 2005) is the only proxy (identified to-date) that accounts

for lagged spawner escapement (i.e. egg deposition) and freshwater egg-to-smolt survival.

The second limitation is the spatial scale of analysis. Survival proxies are generally calculated for large spatial areas only, thus they may overlook important variability at a smaller scale. Nominal salmon catch, PFA and marine productivity are calculated for each country in Europe, and for six regions in North America (ICES 2013). As an illustration of the effect of scale, consider the most recent trend reporting for the ICES regional grouping of Scotia-Fundy (Canada), in which return rate of wild salmon between 1970 and present have been considered stable (ICES 2013). However, within this region, the inner Bay of Fundy has experienced large declines in marine survival (DFO 2008, Gibson et al. 2008) while declines in the adjoining Southern Upland have been less severe and spawner returns remain an order of magnitude higher than the inner Bay of Fundy (Gibson et al. 2011). In the outer Bay of Fundy region, 1SW return rates in the Nashwaak River have averaged 4.95% during the period between 2000 and 2009, whereas mean survival between 1973 and 1982 averaged 5.95% (DFO 2014) – suggesting that survival declines have not been nearly as severe. When observations from these disparate areas are aggregated to form the Scotia-Fundy region, no trend is apparent.

2.4. ECOSYSTEM REGIME SHIFT IN THE ATLANTIC OCEAN

Ecosystem regime shifts have received significant attention in recent ecological research, and the concept is transitioning from its theoretical roots (Holling 1973, May 1977) toward a pragmatic and quantitatively-defensible concept (Collie et al. 2004, deYoung et al. 2004, Andersen et al. 2009). At its core, regime shift theory posits that ecosystems can experience abrupt and persistent shifts from one quasi-stable ecosystem state to a new, quasi-stable state (Scheffer et al. 2001, Beaugrand 2004, Steele 2004, Overland et al. 2008). There is currently no widely accepted definition for regime shift (Hare and Mantua 2000, Mantua 2004, deYoung et al. 2004, Lees et al. 2006, Overland et

al 2008), largely because of ambiguity in the usage of the term and difference in the scope of the fundamental processes to which the term is applied. For the purpose of this review, we define an ecosystem regime shift as abrupt, substantial and persistent changes across multiple (e.g. ≥ 3) trophic levels.

There is now substantial evidence that ecosystem regime shifts have occurred on both sides of the Atlantic in 1989-1990, however the distribution of timing lags among ecosystem components, and potentially also the nature of the causal mechanisms behind the shifts, have differed between the northwest and northeast Atlantic Ocean.

Well documented changes occurred in the early 1990s across much of the northwest Atlantic Ocean, including: the Eastern Scotian Shelf, the Gulf of St. Lawrence, around the Flemish Cap and northern Newfoundland. These changes included: shifts from demersal- to pelagic-dominated biomass, shifts in energy flow, and increased total biomass and overall piscivory (Choi et al. 2004, Bundy 2005, Bundy et al. 2009). Many species (or assemblages of species) across several trophic levels showed large fluctuations of abundance, biomass, mortality rates, recruitment, growth and condition (Carscadden et al. 2001, Choi et al. 2004, Frank et al. 2005, Bundy et al. 2009, Frank et al. 2011). Additionally, the mean trophic level at which organisms fed increased following ecosystem regime shift, largely driven by increased overall piscivory (Bundy 2005).

Most recently, there has been some evidence of a return towards conditions that antedated the most recent regime shift, particularly for the lowermost trophic levels such as zooplankton biomass on the eastern Scotian shelf area of the northwest Atlantic Ocean (Frank et al. 2011, Mills et al. 2013). Therefore it is debatable whether or not this shift will persist and represent a long-term ecosystem regime shift or if the ecosystem will revert to previous conditions and represent only a short-term and widespread ecosystem disturbance.

The late 1990's ecosystem regime shift of the northwest Atlantic Ocean appears to be a result of top-down trophic cascades spurred by persistent over-exploitation of

Atlantic cod (Worm and Myers 2003, Frank et al. 2005, Bundy et al. 2005). This shift was also concurrent with persistent extreme values of the North Atlantic Oscillation index (*hereafter* NAOi), leading some researchers to suggest that the synergistic effects of changes in environmental conditions and overfishing have contributed to persistent low abundance of keystone species (Beaugrand and Kirby 2010).

In the northeast Atlantic Ocean, reorganization of the marine ecosystem occurred in the late 1980s. Changes affecting the ecosystem as a whole, or individual components included: increased primary production (Reid et al. 2001, McQuatters-Gollop et al. 2007), shifting species dominance within the zooplankton community (Beaugrand et al. 2002, Hátún et al. 2009), as well as within small-bodied fish communities (Alheit et al. 2012), biogeographical changes and range extension of plankton and higher trophic level species (Reid et al. 2001, Beaugrand et al. 2009, Hátún et al. 2009, Alheit et al. 2012) as well as phenological shifts (Planque and Taylor 1998, Edwards and Richardson 2004).

Although persistent overfishing has also occurred in the northeast Atlantic Ocean, and may have led to the collapse of some fish species (Reid and Edwards 2001), this is not considered the primary driver of ecosystem regime shift in this area. Therefore, unlike in the northwest Atlantic Ocean, ecosystem regime shifts in the northeast Atlantic region appears related solely to climate effects (Reid et al. 2001, Beaugrand 2004, Beaugrand and Reid 2012). This bottom-up forcing is the result of climate-driven increases in sea surface temperature (SST), reduced turbidity, and freshening of the waters across much of the region (Beaugrand and Reid 2003, Beaugrand 2004, Alheit et al. 2005).

2.5. ATLANTIC SALMON IN A REORGANIZED OCEAN ECOSYSTEM: AN EVALUATION OF POTENTIAL LINKS

The evidence above suggests the existence of a link between ecosystem regime shift and shifts in the marine survival of Atlantic salmon, however the causal mechanisms responsible for survival shifts in Atlantic salmon remain unclear. To date, studies attempting to identify potential causes of these shifts have correlated salmon abundance with climatic, oceanographic or biological variables (e.g. Beaugrand and Reid 2003; 2012, Mills et al. 2013). The use of correlation-based analyses to identify relationships between Atlantic salmon survival and oceanographic/climatic/biological variables is hindered by analytical issues including autocorrelation (Pyper and Peterman 1998) and the fact that correlation does not necessarily imply causation.

The latter issue may be particularly important considering that many ecosystem components show concurrent trends or shifts associated with widespread ecosystem regime shift. Correlating these non-stationary time series (even after detrending) may result in significant associations that signify only indirect causes (sometimes incorrectly referred to as spurious, *sensu* Haig 2003) as opposed to a cause-effect relationship. Recently developed methods to deal with causality in complex ecosystem data show promise, including those with latent variables and short time series (e.g. Sugihara et al. 2012), but have yet to be applied to Atlantic salmon.

A second major limitation of the available correlation-based analyses is that they have focused only on species occupying a lower trophic level relative to salmon while neglecting upper trophic-level predators such as seals, seabirds and cetaceans. Although neither Beaugrand and Reid (2003; 2012) nor Mills et al. (2013) concluded that bottom-up forcing is the causal mechanism affecting salmon, by correlating only those parameters involved with bottom-up forcing, they were unable to assess the relative influence of upper trophic levels on salmon survival. Analyses that involve many trophic levels (e.g. Frank et al. 2005; 2011, Bundy 2005, Bundy et al. 2009) facilitate discussion

regarding the likelihood of top-down vs. bottom-up causal drivers of ecosystem regime shift.

The mechanisms that impact salmon survival and act as potential drivers of survival shifts can be broadly categorized as; (1) the direct effects of climate (which, in addition to impacting ecosystem regime shift, simultaneously impacts salmon survival), and (2) trophic effects resulting from ecosystem regime shift, including alterations in the abundance, distribution and biology salmon prey and salmon predators (also indirectly influenced by climate). Given the difficulties in assessing causal mechanisms of Atlantic salmon survival shifts, in the following section we examine the potential links between correlated variables and discuss any empirical ancillary evidence supporting these links. To facilitate this, we use pre-defined criteria to assess risk (Table 2.1).

The potential impacts of climate on all life-history stages of Atlantic salmon was recently reviewed by Jonsson and Jonsson (2011a), while a review by Friedland et al. (2013) focused specifically on climatic impacts on the marine growth and survival of Atlantic salmon. For this reason, we briefly examine only the most pertinent topics identified by these authors. In contrast, the relationship between salmon survival shifts the effects of trophic interactions (and particularly the role of predation) has received considerable less attention and is the primary focus of the following section. The potential links between the marine survival of salmon and climate-related factors (Table 2.2) and factors related to ecosystem regime shift (2.3) are summarized.

2.5.1. SALMON SURVIVAL IN RESPONSE TO CLIMATE CHANGE

The existence of synchronous trends in abundance among salmon population from a wide geographic area suggests that the factors affecting salmon at sea are widespread and influence mixed-stock assemblages in marine habitats (Friedland et al. 1993, Friedland et al 1998). This is a pattern consistent with the direct and indirect influence of basin-scale climate patterns. There is little question that there have been major

climatological changes over the North Atlantic Ocean and a growing body of literature suggests a relationship between large scale climatic oscillations and Atlantic salmon (e.g. Condrón et al. 2005, Boylan and Adams 2006, Peyronnet et al. 2008, Mills et al. 2013).

Uncertainty remains, however, regarding the spatial scale and variability of this relationship and regarding which indices best predict salmon survival in the ocean (e.g. Friedland et al. 2009a, Beaugrand and Reid 2012). The relationship between climate and ocean conditions varies at continental and regional scales (Fig. 2.3, Hurrell 1995, Visbeck et al. 2001, Stige et al. 2006). Therefore, the relationship between climate and salmon may also vary at similar spatial scales. For example, a positive phase NAO_i leads to elevated SST across much of the ocean off Europe (Visbeck et al 2001; 2003, Drinkwater and Gilbert 2004, Alheit et al. 2005, Weijerman et al. 2005) while the Barents Sea tends to become cooler (Dickson et al. 2002). In the northwest Atlantic Ocean, the Labrador Sea becomes cooler and less saline during positive phase NAO_i (Visbeck et al. 2003, Drinkwater and Gilbert 2004) while the Scotian shelf and the Gulf of Maine experience warming SST and extreme vertical stratification in coastal areas (Visbeck et al. 2001, Drinkwater and Gilbert 2004, Friedland et al. 2012b).

2.5.1.1. Climate impacts on ocean temperature and growth

Climate influence ocean and air temperature, precipitation, the intensity of westerly winds and storm frequency over the North Atlantic Ocean and nearby continental landmasses (Hurrell 1995, Hartley and Keables 1998, Dickson et al. 2002), however, climatic influences on SST are the most direct mechanism linking climate and salmon. Several aspects of the life history and biology of salmon are expected to be impacted by SST, such as; maturation schedules (Saunders et al. 1983, Martin and Mitchell 1985, Friedland and Haas 1996), temperature related stress-induced loss of disease resistance (Fish and Rucker 1945, *see also* review by Ribelin and Migaki 1975) or prevalence and intensity of infection by parasites (Tucker et al. 2000).

Ocean temperature is likely to impact salmon by impacting the relationship between growth and survival. Natural mortality is strongly correlated with body size for

many fish species (Peterson and Wroblewski 1984, McGurk 1986, Gulland 1987, Sogard 1997) and the impact of growth (and consequently body size) on survival is one of the fundamental phenomena driving the recruitment of fishes in the marine environment (Anderson 1988, Miller et al. 1988).

Friedland et al. (2013) recapitulated two decades of research focused on identifying a SST-growth-survival paradigm for Atlantic salmon postsmolts and reported that survival appears to be mediated by growth in the northeast Atlantic Ocean (Friedland et al. 2000, Peyronnet et al. 2007, McCarthy et al. 2008, Friedland et al. 2009a), but not in the northwest Atlantic (Friedland et al. 2005; 2009b, Hogan and Friedland 2010). This highlights the spatially-explicit nature of the factors controlling salmon survival at sea. To date, there has been no investigation of growth-mediated survival for repeat spawning salmon.

Further, temporal patterns in growth inferred from retrospective scale analysis (i.e. patterns captured in the circuli ring spacing on salmon scales) suggests that growth during the summer feeding months governs survival for southern European salmon. Despite a lack of evidence of growth-mediated survival in North American salmon populations, there remains a strong relationship between SST during spring and subsequent salmon returns (Friedland et al. 2003a; 2003b; 2012a), which suggests that ocean conditions when the smolts first enter the sea impacts survival through some yet-unidentified mechanism that overshadows the impact of body size on survival. One hypothesis suggests that the mechanism is related to interaction of climate and the vulnerability of salmon to predation (Hogan and Friedland 2010; Friedland et al. 2012a; 2013).

2.5.1.2. Other climate impacts

Because of the far-reaching impact of climate, salmon may also be affected by climate-driven mechanisms not associated with impacts on growth. Such impacts may include variation in ocean currents and its impact on salmon migration (Friedland et al.

2012b) or the metabolic costs associated with migration, impacts on the phenology of migration (Friedland et al. 2003a, Kennedy and Crozier 2010, Russell et al. 2012, Todd et al. 2012) and potentially via mechanisms that affect salmon while still in freshwater, but ultimately manifest as salmon enter the marine environment (e.g. mean smolt size, Russell et al. 2012). Again, these topics are well reviewed by Jonsson and Jonsson (2011a) and Friedland et al. (2013), who report that there is considerable uncertainty regarding the impact of these mechanisms on salmon survival in the ocean.

For salmon in the northeast Atlantic Ocean, where survival is growth-mediated, access to adequate prey is important. The annual timing for spring smolt emigration from rivers is thought to coincide with the spring phytoplankton bloom period in coastal marine waters, providing maximum food abundance and maximizing fitness (Pearcy 1992, Chittenden et al. 2010, Todd et al. 2012). A decoupling of coherent timing between the seasonal abundance cycles of both predator and prey has been termed a “phenological match-mismatch” (Cushing 1974; 1990), and there is mounting evidence of phenological mismatch between salmon smolt emigration from rivers and the peak spring ocean phytoplankton bloom resulting from recent climate warming. In response to warming climate or recent selection for early run timing, the timing of spring smolt migration has advanced by an average of 3.0 days per decade between 1970 and 2010 for the 31 European populations examined by Russell et al. (2012). Likewise, many phytoplankton species (Edwards and Richardson 2004), and as a result, zooplankton (Edwards and Richardson 2004, Richardson and Schoeman 2004, Ji et al. 2010) now initiate spring blooms earlier in the spring relative to the late 1980s. However, the rate of phenological change is generally considered greater in marine ecosystems compared to freshwater ecosystems (Thackeray et al. 2010), and could therefore establish an expanding phenological mismatch between Atlantic salmon smolts and the spring phytoplankton bloom, potentially reducing food availability for European salmon. Phenological mismatch may also occur for North American populations, with similar run timing advancement (Friedland et al. 2003b, Russell et al. 2012), although the mechanism linking a mismatch and survival is unclear and may reflect vulnerability to predation; not prey availability (Friedland et al. 2012a, Friedland et al. 2013).

Conversely, if we consider the hypothesized dominant role of predation on the survival of salmon in the northwest Atlantic Ocean, the effects of climate-driven changes to ocean currents and the effect of climate on freshwater growth and subsequent size at smoltification are plausible mechanisms affecting the vulnerability of Atlantic salmon to predation. Climate and its variability affects wind direction, wind strength and the strength of ocean currents (Drinkwater et al. 2003, Hurrell et al. 2003, Beaugrand 2004). We possess only a coarse understanding of the marine migration of Atlantic salmon, however, ocean currents appear to influence salmon migration to some extent (Shelton et al. 1997, Dadswell et al. 2010, Friedland et al. 2012b). Using a particle tracking model and wind pseudostress data (i.e. as a determinant of surface currents), Friedland et al. (2012b) showed that the climate-driven changes to prevailing winds in the Gulf of Maine have likely shifted postsmolt migration patterns to the southwest, effectively increasing the duration of time required to exit the Gulf of Maine and exposing salmon to predators for an extended period of time. If similar climate-driven impacts on ocean migration of salmon smolts are widespread in the northwest Atlantic, many populations may experience increased exposure to coastal predators which could, potentially, decrease salmon survival.

Climate change-induced warming of river temperatures appears to have increased growth rates of salmon parr (Jonsson et al. 2005), resulting in younger (ICES 2009) and smaller smolts (Scott 2001, Russell et al. 2012) at the time of ocean-entry. Body size is an important determinant of survival in many marine fishes (Gulland 1987, Sogard 1997) however, despite some evidence of size-selective survival in estuaries and coastal habitats (e.g. Salminen et al. 1995, Davidsen et al. 2009, Halfyard et al. 2013), the relationship between smolt size and subsequent adult returns remains unclear. There is evidence of a positive correlation between smolt size and survival to adult in several Scandinavian stocks (Salminen et al. 1995, Kallio-Nyberg et al. 2004, Saloniemi et al. 2004, Jutila et al. 2006, Jokikokko et al. 2006), and in some other, but not all, European populations (Friedland et al. 2009a). The relationship between smolt size and subsequent marine survival is consistent with aforementioned paradigm of growth-mediated survival for European populations. The effect of smolt size on the survival of North American salmon

is unclear, and with the exception of preliminary, small scale examinations (Ritter 1972, 1975), has not been well assessed. Given the lack of relationship between growth and marine survival, larger smolts are not expected to produce increased marine return rates, perhaps with the exception of survival within estuaries.

These alternative relationships between climate and Atlantic salmon may be important drivers of reduced survival of Atlantic salmon. However, our current state of knowledge on these topics does not permit a full evaluation of their likelihood, nor their impact on populations.

2.5.2. SALMON SURVIVAL IN RESPONSE TO ECOSYSTEM REGIME SHIFT

In response to widespread ecosystem regime shift, the abundance, distribution and behaviour of other many marine species has been affected. In addition to being similarly affected by the drivers of ecosystem regime shift (i.e. climate), Atlantic salmon have also likely been affected by ecosystem regime shift via trophic interactions. More specifically, changes to the availability of their prey (e.g. via altered prey abundance or competition for prey) and the effect of the altered abundance and ecology of their predators has likely led to decreased marine growth and increased predation-related mortality, respectively.

2.5.2.1. Altered prey abundance, distribution or species

Along with temperature, the availability of prey is a primary determinant of salmon growth, and changes in the food web upon which salmon at sea depend could reduce growth, and ultimately, survival. Bottom-up control via altered prey resources is likely to impact Atlantic salmon by: a) altering the abundance of important prey species, b) affecting the quality of the available prey, c) altering the abundance of intraspecific competitors, or d) shifting the relative competitive advantages between salmon and other species. However, after consideration of the evidence for a growth-survival relationship, prey-driven survival of virgin Atlantic salmon is likely only in the northwest Atlantic

Ocean (*see* discussion above). The relationship between prey abundance and the survival of repeat spawners remains unclear but is discussed below.

In the Northeast Atlantic Ocean, there is evidence of strong associations between time series of SST, northern hemisphere air temperature, the NAO i , and abundance indices of phytoplankton (continuous plankton recorder), zooplankton (colour) and nominal commercial catch of Atlantic salmon (Beaugrand and Reid 2003, 2012). The authors interpreted variable lags in the response of each biological parameter as an upward trophic cascade, however, they note that this association does not necessarily equate to bottom-up regulation of the abundance of salmon, and that the abrupt shift in salmon catches may be related to broader ecosystem regime shift via other mechanisms. None the less, these relationships are consistent with bottom-up effects and the hypothesis that the survival of European Atlantic salmon is growth-mediated, which would consequently be sensitive to prey availability. Recent abrupt declines in the abundance (and potentially quality) of prey items could lead to an abrupt decline in salmon growth, and consequently, survival.

Identifying trends in the abundance of salmon prey is difficult given the highly variable diet of Atlantic salmon, however, it is useful to consider only those species available to salmon given our knowledge of where salmon are distributed during the spring and summer (e.g. feeding grounds in the Norwegian Sea or West Greenland during the summer and autumn; Thorstad et al. 2011b). As a generalization, much of the salmon diet is derived from pelagic prey resources (*see reviews by* Jacobsen and Hansen 2000, Rikardsen and Dempson 2011, Dixon et al. 2012). Potentially important prey items in the northeast Atlantic are the zooplankters *Calanus finmarchicus* and *Euphasid* species (*see* Haugland et al. 2006), which are strongly correlated with SST, northern hemisphere air temperature and climate (e.g. Fromentin and Planque 1996, Friedland et al. 2009a, Beaugrand and Reid 2013). There is evidence of positive shifts in the all-species abundance of phytoplankton, and negative shifts in the all-species abundance of zooplankton across much of the northeast Atlantic Ocean, the timing of which occurred

in the late 1980s and potentially again around 1996/1997 – similar to shifts in salmon survival (Beaugrand and Reid 2003; 2012).

As salmon grow, fish constitute a larger portion of their diet (Hislop and Shelton 1993, Jacobsen and Hansen 2000; 2001) and as such, Atlantic salmon at sea “feed up the food chain” ontogenetically (Pimm 2002). Fish species such as sand lance *Ammodytes* spp., and the juvenile stages of herring *Clupea harengus*, and various gadoids may also be important to salmon (Jacobsen and Hansen 2000, Rikardsen et al. 2004, Rikardsen and Dempson 2011). There is conflicting evidence on trends in the abundance of potential prey fishes, although the available abundance time series are limited. For example, the number of gadoid recruits have experienced an overall decline in the North Sea, remaining low since the late 1980s (Beaugrand 2004; Kristiansen et al. 2011) while cod recruitment elsewhere in the northeast Atlantic has been variable and without a widespread pattern (Stige et al. 2006, Kristiansen et al. 2011). Alternatively, the abundance of Norwegian herring stocks have rapidly increased since approximately 1990 (Toresen and Østvedt 2000, Edwards et al. 2013). Long-term time series of abundance are not available for sandeels in the northeast Atlantic Ocean.

It is most probable that salmon rely not on a single species, but rather on a broad prey community because Atlantic salmon postsmolts are opportunistic feeders with substantial spatial and temporal variation in their diet (Rikardsen et al. 2004, Haugland et al. 2006, Rikardsen and Dempson 2011). Thus, relationships with any single prey fish species may not be obvious and associations between salmon survival shifts and the abundance of prey fishes are likely to be inconspicuous.

The quality of prey (e.g. size, species of varying energy density) may also be important for salmon growth. Given the limited diet data available for salmon at sea, it is difficult to assess whether a change in the quality of the salmon’s diet has occurred following ecosystem regime shift. However, changes in prey quality have been noted for other pelagic-feeding fishes of the northeast Atlantic Ocean. For example, decreases in abundance of the large zooplankton preferred by Baltic herring resulted in a 50%

reduction in size at maturity in the Baltic Sea (Flinkman et al. 1998). The reduction of large zooplankton abundance occurred at a time when total zooplankton biomass was increasing, largely due to shifting species composition forced by warmer and less saline conditions (Aleksandrov et al. 2009). Similar impacts are plausible for Atlantic salmon.

Bottom-up forcing associated with trophic cascades has been reported for other fishes in the northeast Atlantic, such as the recruitment of gadoids which has largely declined following ecosystem regime shifts (Beaugrand 2004, Beaugrand and Kirby 2010, Johannessen et al. 2012). Similarly, Hátún et al. (2009) reported increased catches of piscivorous pilot whales *Globicephala melas* in the Faroe Islands and related this to altered migration patterns of the whales in response to changes in the abundance and distribution of their prey.

Thus, the weight of evidence in the northeast Atlantic ocean supports the hypothesis of Friedland et al (2009a) that the marine survival of virgin Atlantic salmon appears to be closely linked to growth during the postsmolt year, where growth appears driven by bottom-up direct interaction with temperature and indirect interaction with prey production (in particular zooplankton), and growth-mediated interactions with predators.

Although a growth-survival relationship has not been established for repeat spawning Atlantic salmon, there is some evidence that prey-availability could be a primary determinant of their marine survival. Further, the fact that repeat-spawning salmon may be capable of avoiding most predators (Chaput and Benoît 2012) suggests that prey availability could be relatively more important for survival than predation. Prey availability may account for observed recent positive shifts in the survival of repeat spawners from the Miramichi River. Here, the return rate of consecutive repeat spawners was correlated with the abundance of small bodied fish in the Gulf of St. Lawrence (Chaput and Benoît 2012). The authors suggested that bottom-up control drove survival, and noted that the abundance of the smallest potential prey fishes (<10cm) and salmon survival both rose sharply in the mid-1990s. Further, a shift toward a zooplanktivore-dominated ecosystem state with increases in the abundance of known salmon prey (e.g.

capelin, rainbow smelt, barracudina and herring) may also have contributed to increased survival (Chaput and Benoît 2012). However, similar to the correlation analyses for virgin spawners, associations between the survival of repeat spawners and the abundance of small fishes is complicated by the widespread response of marine species to ecosystem regime shift and these associations may not reflect a cause-effect relationship.

The survival of repeat spawning salmon may be driven by diverse and localized factors. For example, the Miramichi River, NB and Lahave River, NS, Canada are separated by only ca. 300 km but show divergent survival trends. There is some evidence that the biomass of small planktivorous fishes also increased following ecosystem regime shift on the eastern Scotian shelf of the northwest Atlantic Ocean, particularly for species important as salmon prey (Bundy et al. 2005; 2009), and consequently would not support the idea of prey-driven survival of repeat spawners for this population.

2.5.2.2. *Altered predator abundance, distribution or behaviour*

Salmon mortality in the ocean is thought to be highest before the first winter at sea, and predation is suspected to be an important driver of survival rates (Salminen et al., 1995, Hansen and Quinn 1998, Hansen et al. 2003, Potter et al. 2003). The diversity of potential marine predators has been reviewed by several authors (e.g. Hislop and Shelton 1993, Hansen et al. 2003, Cairns 2006), and in general, the relative importance of these taxa varies geographically and spatially and dependant on the age of salmon. A brief synopsis of pertinent predation in marine environments is presented below.

Several bird species are known to prey upon postsmolts in estuaries and in the ocean. For example, double crested cormorants *Phalacrocorax auritus*, and to a lesser extent great cormorants *P. carbo*, have been widely suggested as potentially significant predators of postsmolts in estuaries (Milton et al. 1995, Dieperink et al. 2002, Koed et al. 2006). Postsmolts may constitute a significant portion of the diet of cormorant (e.g. approximately 35-45% occurrence, 20-60% volume/mass) when the birds are foraging near salmon rivers during smolt outmigration, but much less at other times or locations

(Cairns 1998). In the open ocean, northern gannets *Morus bassanus* are known predators of postsmolts through the summer period (Montevecchi et al. 2002; 2009, Montevecchi and Cairns 2007). Although gannets show significant inter-annual diet variability presumably related to prey availability (Garthe et al. 2011, Montevecchi et al. 2009), salmon are common prey item (Montevecchi and Myers 1996, Montevecchi and Cairns 2007, Montevecchi 2007).

Piscivorous fishes also prey upon salmon. Predation on postsmolts by demersal fishes (e.g. Atlantic cod *Gadus morhua*, and saithe *Pollachius spp.*) in European estuaries is well documented (Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1988, Hislop and Shelton 1993, Jepsen et al. 2006, Hedger et al. 2011), however, the role of demersal piscivorous fishes as predators of salmon in the northwest Atlantic Ocean remains unknown. Pelagic fishes also consume postsmolts, most notably striped bass *Morone saxatilis* (Beland et al. 2001), and also presumably spiny dogfish *Squalus acanthias* (Friedland et al. 2012b) which have been implicated in predation of Pacific salmon (Beamish et al. 1992).

Finally, mammalian predators may also be important consumers of Atlantic salmon, including odontocetes (Wilson et al. 1997, Janik 2000, Santos et al. 2001) and pinnipeds; the latter of which have been the focus of several predation-related studies. In the open ocean, the prevalence of salmon in diets of pinnipeds is generally very low (<1%; Hammill and Stenson 2000), however, these estimates may be unreliable due to the infrequency of salmon as prey, and the resulting large number (e.g. tens of thousands) of stomach samples required to achieve reasonable confidence in quantitative estimates of the portion of salmon in marine mammal diets at sea (Amiro 1998, Cairns 1998). Obtaining and analyzing sufficient sample sizes would be difficult. Additionally, the estimates are biased due to the sampling of seals at times and locations where salmon are unlikely to occur (Matejusová et al. 2008).

Indirect evidence also suggests that seals may be important salmon predators. On Sable Island, Nova Scotia, Canada, Bowen et al. (2002) used video cameras attached to

39 harbour seals to record foraging activity and interactions with prey between 1995 and 1997. From a total of 1094 prey, there was a single Atlantic salmon-seal interaction. Given the low abundance of salmon in the southern northwest Atlantic Ocean during the mid-1990s (ICES 2013), and the limited sampling frequency (~ 3 hours of tape per seal), one might expect that the likelihood of such an encounter would have been exceedingly low for individual seals. Considering the large number of seals present in the region, cumulative predation on salmon could be high.

Unlike the case in the open ocean, seal diets in estuaries or near-shore coastal areas may contain a significantly greater proportion of salmon. Atlantic salmon and anadromous brown trout *Salmo trutta* contributed up to 59% (by mass) of harbour seal diet in a Scottish estuary during the peak of the salmon run (Middlemas et al. 2006). Several other papers report lower estimates (*see* Sharples et al. 2009), however, these bone-based estimates may underestimate the fraction salmon in predator diets. Emerging DNA-based techniques for diet analysis may be able to provide more reliable estimates (Matejusová et al. 2008).

With the exception of short or seasonal periods, salmon are not known to be an important prey species for any predator. However, even infrequent opportunistic predation by individual predators could lead to a substantial salmon population-level mortality rate if predator abundance is high. For example, Cairns and Reddin (2000) estimated that if harp seals (ignoring other seal species) of the northwest Atlantic consumed 100% of the annual North American postsmolt production, salmon would represent only 0.09% of the harp seal diets.

Quantifying the population-level impact of estuarine or marine predation is a daunting task, however, there are some estimates of the total number of salmon consumed over short time periods. For example, cormorants in the River Bush, Ireland consumed between 665 to 1,240 salmon smolts per day during the smolt run, and Kennedy and Greer (1988) estimated that cormorants might remove as much as 51-66% of the total wild smolt run and between 13-28% of the hatchery smolts released into that river.

Similarly, Milton et al. (1988; 1995) used river-specific cormorant diet data collected in two Nova Scotia (Canada) rivers and their estuaries to estimate that cormorant predation removed 0.8% to 12.9% of wild smolts and 6.2% to 16.7% of hatchery smolts released to the river. Piscivorous fishes may consume up to 50% of smolt production in the lowermost sections of some Swedish rivers (Larsson 1985). These studies focused largely on river and estuarine habitats, thus the consumption of postsmolts in coastal areas or the open ocean, and the effects of this predation on return rates is unknown.

Based on patterns of acoustic tags detections in four Nova Scotia estuaries, Halfyard et al. (2012) estimated that between 75-100% of the total mortality occurring in estuaries might be attributable to avian predation (chiefly double-crested cormorants). Applying this rate to their estimates of total mortality, avian predation may have removed between 22.0 and 57.6% of the total smolt production at the four study sites. Similar estimates of predator-induced losses have been estimated for cod, saithe and anadromous brown trout, where an estimated 24.8% of the smolt run from the River Surna, Norway was consumed (Hvidsten and Møkkelgjerd 1988). Fish predators in the River Orkla, Norway were estimated to consume up to 20% of the total smolt production (Hvidsten and Lund 1988), and the authors noted that wild- and hatchery-origin salmon were equally likely to be consumed.

The northern gannet colony on Funk Island, Newfoundland, Canada, is the fourth largest colony in the northwest Atlantic Ocean (Montevecchi et al. 2002). Using a stochastic bioenergetics model and a high quality gannet diet time series, Montevecchi et al. (2002) estimated that this single colony consumed 0.2% of the annual estimated North American biomass of Atlantic salmon from 1977 to 1989, and as much as 2.7% of the annual estimated biomass of Atlantic salmon between 1990 and 2000.

Hammill and Stenson (2000) estimated total prey consumption by four seal species (harp, hooded, harbour and grey) in Atlantic Canada. Bioenergetic modelling estimated that annual consumption of salmon smolts by the four species increased linearly between 1990 and 1996, and ranged from approximately 2500 to 3200 tons.

Cairns and Reddin (2000) used the best available diet data to estimate total consumption of salmon by several marine predators in eastern Canada, including four species of seal and several marine bird species. Their estimates were, however, wildly variable and in some cases (e.g. grey seal, *Halichoerus grypus*) estimated consumption that exceeded the number of Atlantic salmon at sea (153.1% of total estimated salmon biomass).

The utility of empirical estimates of salmon consumption in the ocean may be limited by their short temporal scope or the quality of diet data (Cairns and Reddin 2000) or assumptions regarding the relative biomass of salmon in the ocean compared to other potential other prey for salmon predators (McGurk 1986). However, if we consider the widespread belief that salmon mortality in the ocean is independent of density (Jonsson et al. 1998, Jonsson and Jonsson 2004, *but see* Friedland et al. 2009b), then all predation-related mortality incurred here would be additive and result in reduced marine return rates (Ward and Hvidsten 2011). As such, it is important to continue assessment of the potential role of predation as a causal mechanism of shifts in the marine survival of Atlantic salmon. We propose a theoretical approach based on 1) abundance trends in predator populations, and 2) the functional response of salmon predators. These criteria are discussed below.

The abundance of many potential marine salmon predators has fluctuated dramatically in the North Atlantic Ocean, as a result of exploitation and as a result of ecosystem regime shift. Variable predator populations may impact predation pressures on Atlantic salmon. For example, the previously-mentioned collapse of Atlantic cod stocks has reduced the abundance of this potentially important predator in much of the North Atlantic Ocean (e.g. Bundy 2005, Brander 2007, Bundy et al. 2009, Frank et al. 2011). In addition to declines in populations of several other demersal piscivores (Bundy et al. 2009, ICES 2012a), this may lead to decreased predation pressures from these fishes, although our knowledge of postsmolt predation by demersal fishes is largely confined to estuaries and fjords in the Scandinavian countries (e.g. Hvidsten and Lund 1988, Jepsen et al. 2006, Hedger et al. 2011), therefore the benefits of decreased predation in the northwest Atlantic region remain speculative.

Alternatively, the abundance of many other potentially important salmon predators has increased. For example, grey seal populations in the northwest Atlantic Ocean have increased at an exponential rate of approximately 13% per annum since the 1960s (Fig. 2.4a; Hammill et al. 1998, Bowen et al. 2003, Trzcinski et al. 2009), with population growth slowing only recently (Bowen et al. 2007). As expected, the total estimated biomass of food consumed by grey seals has also increased dramatically (Bundy 2005). Grey seals from the major Canadian colonies (Bowen et al. 2007) disperse in the spring and feed over a large area of the northwest Atlantic Ocean (Bowen et al. 2006, Breed et al. 2009), thus, there is likely significant overlap in the distribution of grey seals and North American Atlantic salmon. Similarly, harp seal abundance in the northwest Atlantic Ocean recently exceeded seven million animals – the highest abundance in known history (Fig. 2.4a; Hammill et al. 2013).

Trends in seal abundance are more variable in the northeast Atlantic Ocean. Some small grey seal populations have experienced declines, although abundances of all the major grey seal herds (e.g. Scotland, the Baltic Sea and northeast England) are increasing (Fig. 2.4b; Thompson and Härkönen 2008, Thomas 2013). The other major seal species in this area is the harbour seal, whose populations declined following outbreaks of phocine distemper virus in the late 1980s and again in the early 2000s (Fig. 2.4b). In the few populations where abundance data exists since the 1970s, populations appear to have fluctuated although mean abundance has remained unchanged (Lonergan et al. 2007).

Abundances of other important salmon predators have also increased in recent years. For example, the abundance of northern gannets has increased at several major rookeries in the northwest Atlantic Ocean, most growing between 50-100% between the period of 1972 and 1999 (Fig. 2.5, Montevecchi et al. 2002). Similarly, the abundance of northern gannets across Europe has increased, and the abundance of those breeding in the United Kingdom increased by 88% between 1970 and 2002 (Mitchell et al. 2006). Other bird predators of interest have shown mixed population trajectories. Since the 1970s, great cormorants in Britain and Ireland have increased by approximately 44% while double-crested cormorants have declined by ~5% (Mitchell et al. 2006). In the northwest

Atlantic, population abundance of cormorants is uncertain; however, some estimates from Nova Scotia show that between 1972 and 1992, populations of great cormorants and double-crested cormorants increased by approximately 80% and 190%, respectively (Milton et al. 1995), although few recent estimates exist.

The abundance of spiny dogfish *Squalus acanthias* L., also appears to have increased in the northwest Atlantic Ocean, with an average spring biomass of approx. 200 000 metric tonnes in the 1980s, to a peak of approx. 500 000 Mt in the early 1990s and have remained at approx. 300 000 Mt since (Campana et al. 2007).

In addition to increased population abundance, the distribution of some salmon predators may also have shifted, resulting in localized changes of predator abundance and presenting new predator fields to Atlantic salmon at sea. Warming SST in the Gulf of Maine and south of Cape Cod, USA shifted the distribution of some potential postsmolt predators (e.g. spiny dogfish, Friedland et al. 2012b). As a result, return rates to the nearby Penobscot River correlate with the intensity of spring winds and trends in potential predator abundance, potentially indicating the hypothesized dynamic of altered migration pathways that lead to increased interaction with more and novel predators (Friedland et al. 2012b).

Atlantic salmon constitute only minor portions of the diet of most marine salmon predators (Cairns 1998), and thus these predators are not likely dependent on, or exhibit a population-level response to salmon abundance. Predator abundance is likely, therefore, to fluctuate with the abundance of alternative prey (i.e. non-salmon prey). Termed a numerical response (*sensu* Solomon 1949), predator abundance may increase by: 1) increased reproductive output associated with abundant prey, leading to predator population growth (i.e. bottom-up control of predator population), or 2) increased density in localized areas as predators concentrate their effort where prey density is highest (i.e. an “aggregative response”, Hassell and May 1974). When predator abundance increases (driven by the abundance of non-salmon prey), non-selective predators that prey upon salmon opportunistically may exert significant population-level mortality on Atlantic salmon. Likewise, even stable predator abundance can severely affect depleted (small) salmon populations if predation pressure (e.g. search rate) is independent of salmon

abundance, effectively increasing the population-level rate of predation – a highly destabilizing dynamic (Ward and Hvidsten 2011), that can lead to extirpation of small populations.

In addition to changing predator abundance, changes in the functional response of predators may also lead to altered predation intensity. The functional response of a predator describes the way that per capita rate of prey consumption changes in response to prey availability. There are three types of functional response (Holling 1959), although only two are expected from Atlantic salmon predators. Predators with a type II functional response exhibit a constant search rate, therefore as prey density increases, so too does the number of prey consumed per predator (Fig. 2.6a). Predators exhibiting a type III functional response vary their search activity with prey density, where predators faced with abundant prey increase their search rate. Therefore, mortality of prey is low when populations are low, mortality then increases with population density up to a threshold, after which predators are consuming prey at their maximum rate (Fig. 2.6b).

The functional response of predators in direct response to Atlantic salmon is likely relevant to Atlantic salmon marine survival only in estuaries where salmon are at a sufficient density to warrant predator concentration (seasonally). Seals, piscivorous fishes and birds are known to aggregate as postsmolt or adults migrate through estuaries (e.g. Middlemas et al. 2006, Hedger et al. 2011, E.A. Halfyard *unpublished data*).

Alternatively, the density of Atlantic salmon in the open ocean is very low relative to other marine pelagic species; therefore predation rates on salmon are likely altered as predators respond to changes in their entire prey field. If salmon predators preferentially focus on more abundant species and ignore Atlantic salmon (i.e. a type II response), some reprise may occur for Atlantic salmon. However, most salmon predators are generalist feeders in the ocean and are likely to exhibit some consistency in their forage activities (i.e. a type II response). Therefore, even incidental predation by a large predator population (sustained by other, more abundant species) has the capacity to produce high salmon population-level mortality (Fig. 2.6b). There is emerging evidence that some

important avian postsmolt predators have altered their diet in response to ecosystem regime shift.

Marine birds are considered favorable bioindicators of fish abundance and marine ecosystem state (Cairns 1987, Montevecchi 1993, Piatt et al. 2007). One of the more studied indicator bird species has been the northern gannet. Atlantic salmon constituted only a minor portion of gannet diet through much of the late 1970s and 1980s, however, their prevalence increased during the 1990s, and salmon apparently became an important staple of gannet diets in the last decade (Fig. 2.7, Montevecchi 2007). The greatest rate of predation on postsmolts occurred in 2002 when 32% (by mass) of gannet diets was salmon. The reason for this shift is thought to be related to oceanic conditions and their effects on the abundance of the gannet's primary prey (capelin). In cold years, the absence of warm water prey (e.g. mackerel, herring and squid) and unavailability of capelin forced gannets to forage further offshore, spend more time transiting to foraging areas, alter their diving/feeding behaviour, and ultimately target Atlantic salmon (Montevecchi 2007, Montevecchi et al. 2009, Garthe et al. 2011). It is unclear whether the observation of a shifting diet applies to other gannet populations, as gannets from more southern colonies use different foraging strategies and have substantially different diets (Garthe et al. 2007). This may reflect the diversity of prey resources in the southern Gulf of St. Lawrence, and as such, consistently available non-salmon prey may attract the most gannet attention, effectively shielding the relatively rare Atlantic salmon (e.g. Garthe et al. 2007).

Like gannets, coastal feeding cormorants may also be responding to ecosystem regime shift in the northwest Atlantic Ocean and may prove to be good indicators of ecosystem state. As previously mentioned, the ecosystem in this region transitioned from one dominated by demersal and benthic fishes to one dominated by the pelagic community. The diet of cormorants in the Gulf of St. Lawrence also appears to have shifted from a diet dominated by benthic species to one dominated by pelagic species (Rail and Chapdelaine 1998). As a result, the likelihood of cormorant encounters with Atlantic salmon is relatively high for pelagic-foraging cormorants compared to those

targeting benthic species. Similarly, Boström et al. (2012) suggested that great cormorants in Sweden have shifted diet in response to altered fish communities; however, their data are limited to two years and may not adequately encapsulate inter-annual variability.

Unlike seabirds, there is little evidence to suggest that seal diet in the northwest Atlantic has shifted to incorporate more pelagic fishes as a result of ecosystem regime shift. Bowen et al. (2006) provided one of the most comprehensive time series of seal diets available, covering the period 1993 and 2001. Although there has been substantial inter-annual variability, the ratio of demersal to pelagic prey does not appear to have shifted over this time period. The diet of grey seals prior to the widespread ecosystem regime shift of ~1990 has been poorly assessed.

Although not related to a functional response observed in seal diets, there is circumstantial evidence that increased seal abundance has led to increased seal-salmon interactions. For example, the prevalence of wounds (presumed seal bite marks) on Atlantic salmon returning to the Penobscot River, ME, USA has increased from <0.55% between 1970 and 1985, to as much as 8 to 11% in the mid-1990s (Baum 1997). Similar wounds have been reported elsewhere (e.g. Thompson and MacKay 1999, ICES 2012b). Variability in the state of healing of wounds suggests that predation occurs during several stages of the migration and likely over large areas (ICES 2012b) although the relative scarcity of wounding on fall-run fish (Baum 1997, ICES 2012b) suggests that these late migrants may not be subject to the same level of predation.

Salmon wounds document attempted predation events where the salmon survived both the capture attempt and the physical trauma of the wound long enough for observation. Extrapolating wounding rates to estimate the encounter rate between predators and salmon at sea is difficult because the capture efficiency of predators in pursuit of salmon is unknown. However, if it is assumed that the capture efficiency has not changed through time, the quantification of wound prevalence may provide a reasonable index for the frequency of encounters between seals and salmon.

It is important to note that the timing of population increases for seals and seabirds in the northwest Atlantic Ocean precede ecosystem regime shift. Energy flow pathways sustaining these predator populations has likely changed as a result of ecosystem regime shift (Bundy 2005), thus the effect of predation pressures on Atlantic salmon are similarly likely different pre- and post-ecosystem regime shift. Further, as a result of the difficulty in quantifying the functional response of predators to ecosystem regime shift and the potential non-linear nature of ecosystems (May 1986, Stenseth and Myrseth 2002), identifying associations between predator abundance and salmon survival is not likely possible. None the less, the weight of evidence would suggest that predation pressures exerted upon Atlantic salmon at sea appear to increase following ecosystem regime shift.

2.6. CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

The marine survival of Atlantic salmon has declined over the last three decades, and these declines appear to have been abrupt, significant and likely represent persistent shifts. Although these shifts have been formally identified for virgin spawning Atlantic salmon (smolt-to-spawner survival), there is also evidence of a similar survival shift for repeat spawners (spawner-to-repeat spawner survival). The relationship between ecosystem regime shift and survival shifts have not been widely investigated in repeat spawning salmon despite the importance of the egg deposition from repeat-spawners for maintaining many wild salmon populations (Saunders and Schom, 1985, Chaput and Jones 2006, Niemelä et al. 2006). On both sides of the North Atlantic Ocean, shifts in the survival of virgin salmon have been concurrent with ecosystem regime shift while the survival of repeat spawning salmon appears to lag behind ecosystem regime shift.

There is evidence that climate may be directly responsible for survival shifts via warming ocean temperatures and its effect on growth, and also potentially via other mechanism such as driving phenological mismatches, altering ocean currents and causing effects in freshwater that impact marine survival. European salmon appear most affected

by SST during the late summer and autumn in ocean feeding areas (Friedland et al. 2009a) while North American salmon appear most affected by early spring SST in coastal areas (Friedland et al. 2003b, Friedland et al. 2013). Salmon growth is affected by SST, and there is strong evidence of growth-mediated survival in the northeast Atlantic waters whereas survival of salmon in the northwest Atlantic region is not growth-mediated (Friedland et al. 2013).

Salmon also appear to have been affected by ecosystem regime shifts via altered trophic structure. In the northeast Atlantic, prey availability appears to have decreased following widespread ecosystem regime shift and, because salmon abundance and survival is conditional upon growth (which is affected by prey availability and favorable ocean temperatures), reduced prey availability has probably reduced both growth and survival.

Predation may also be important, particularly for North American origin salmon. The abundance of many important predators has increased in the northwest Atlantic Ocean and there is some documentation of a functional response of predators – both of which would increase salmon mortality. Conversely, the abundance of the major salmon predators appears to have remained largely constant in the northeast Atlantic Ocean, and a functional shift in predator behaviour has yet to be described in this region. Therefore, predation is most probably the primary driver of salmon survival shifts in the northwest Atlantic Ocean; however, there is little reason to believe that predation alone has caused a shift in marine survival – thus supporting the finding of growth-mediated mortality (Friedland et al. 2009a). In North America, predation pressure appears to be controlled by the interaction of predator abundance, predator behaviour and ocean conditions in the spring (potentially representing a climate: predator synergism). Predation pressure appears to have increased following widespread ecosystem regime shift.

In trying to synthesize this review, it is difficult to formulate a cohesive synopsis that generalizes trends in the marine survival of salmon and clearly defines the links with ecosystem regime shifts. There is considerable evidence that the marine survival of

salmon has experienced an abrupt shift in many populations, sea ages and origins (wild or hatchery), however, there was also evidence that not all populations were impacted equally, with variability in the direction (i.e. increased or decreased survival), magnitude, and the timing of these shifts. Further, the evidence of linkages with causal drivers of marine survival shifts is similarly variable.

A likely explanation for this variability is the significant population- and regional-level variation in Atlantic salmon ecology, with localized climate effects, variable prey and predator fields, and likely variable other threats faced by salmon in different parts of their distribution. For example; if 1SW and 2SW salmon occupy different marine habitats (and there is reason to suspect this is true, *see* Jonsson and Jonsson 2004, Chaput and Benoit 2012), then the ocean conditions, prey availability and predator fields faced by these two groups is likely also different. This variability is important because it challenges the current paradigm that declines in the marine survival of Atlantic salmon are the result of a common threat that occurs in habitats shared by all populations and life stages. Accounting for this variability, through region- or population-specific conservation programs will increase the likelihood of population recovery.

This review is also informative as it highlights the potential timing of important marine mortality. The earliest portion of the marine phase is important for North American Atlantic salmon as climate effects occur in spring and early summer while salmon are in estuaries and coastal habitats, and many of the trophic-mediated impacts of ecosystem regime shifts (e.g. predators concentrated near estuaries, coastal areas) appear to largely occur within the first few months at sea. In Europe, climate-related effects appear to occur slightly later (i.e. by late summer) and trophic-mediated impacts of ecosystem regime shift (i.e. growth-mediated relationships with prey species on the feeding grounds) also appear to occur on a similar time scale. Further, evidence of changes in the abundance of salmon predators, their foraging behaviour (functional responses) and salmon prey is largely focused on this early marine period.

Our knowledge of marine mortality comes largely from data (e.g. return rates) that are calculated for the entire marine residency of the fish. Thus, by partitioning the marine phase into this early portion (sea entry to summer in North America and sea entry to fall in Europe) and then the remaining marine phase, future research can focus on this early phase; which is convenient for researchers owing to increased physical accessibility, more defined spatial bounds and a clear seasonality to their use by various salmon life stages.

The implications of shifts in the marine survival of Atlantic salmon and the influence of climate and ecosystem regime shift are not yet fully understood. Given the projections of continued climate warming (e.g. Meehl et al. 2007), Atlantic salmon are likely to continue entering a warmer ocean that is unfavorable to high survival. Further, unless the effects of ecosystem regime shift are reversed, altered ocean ecosystems are likely to impact salmon prey and predator abundance, which in turn could affect salmon survival and population persistence.

Unlike many threats impacting salmon in freshwater which are amenable to mitigation (e.g. liming to mitigate the effects of acid precipitation, Sandøy and Romundstad 1995, Sandoy and Langaker 2001), the issues influencing Atlantic salmon survival at sea will require comprehensive and holistic approaches such as international reductions on greenhouse gas emissions and ecosystem-based fisheries management. These management strategies are likely to require decades to implement and even greater time to show benefits for Atlantic salmon. In the interim, conservation measures that provide even marginal increases in marine survival, such as reducing predation within the confined environment of estuaries, may increase the likelihood of population persistence. Further, the conservation of genetic and life-history diversity of wild salmon populations (e.g. Garcia de Leaniz et al. 2007) should maximize the likelihood that Atlantic salmon will persist in this changing and unfriendly ocean environment.

Table 2.1 - Criteria for deriving a causal certainty ranking.

Causal certainty ranking	Evidence	Quantifiable impact on survival	Description
Unknown	None	No	Unsubstantiated, but plausible link between the mechanism and salmon populations.
Low	Direct	No	Plausible link with scientific evidence suggesting that the mechanism DOES NOT affect salmon populations.
Moderate	Indirect	No	Plausible link with limited evidence that the mechanism can affect salmon populations.
High	Direct	No	There is scientific evidence linking the mechanism and salmon populations.
Very High	Substantial	Yes	Very strong scientific evidence that mechanism occurs and the magnitude of the impact to populations can be quantified.

Note: The causal certainty outlines the strength of evidence linking the specific mechanism to the observed shifts in the marine survival of Atlantic salmon; it does not reflect the overall potential importance of the mechanism. Evidence of the mechanism reflects the availability of published literature; either direct evidence examining the links between salmon survival and the mechanism specifically, or indirect evidence examining the mechanism but not necessarily the relationship between with salmon. The evaluation of a plausible link requires that there is a clear and ecological sound pathway for the mechanism to affect Atlantic salmon.

Table 2.2 – Climate-related potential causal mechanisms that may have caused the observed shifts in salmon return rates and/or contributed to continued low return rates.

Specific Causal Mechanism	Plausible Link	northwest Atlantic Ocean		northeast Atlantic Ocean	
		Evidence	Causal Certainty	Evidence	Causal Certainty
Effects of climate variability					
Influences on salmon growth	Climate has affected SST, which impacts salmon growth directly, represening a SST:growth:survival paradigm.	To date, there has been no evidence of a positive growth-survival relationship in postsmolts (1,2,3). Not assessed for repeat spawners.	LOW (virgin) UNK (repeat)	A strong growth-survival relationship has been established (4,5,6,7). Not assessed for repeat spawners.	VERY HIGH (virgin) UNK (repeat)
Phenological mismatch	The timing of smolt migration has changed such that salmon miss the optimal window for survival.	The timing of smolt outmigration has advanced (8,9) slower than coastal SST (9,10), but the impact on survival remains unquantified. Not assessed for repeat spawners.	HIGH (virgin) UNK (repeat)	The timing of smolt outmigration has advanced (8), and coastal SST warms earlier (11, 12,13), but the impact on survival remains poorly assessed. Not assessed for repeat spawners.	HIGH (virgin) UNK (repeat)

Note: (1) Freidland et al. 2005, (2) Friedland et al. 2009b, (3) Hogan and Friedland 2010, (4) Friedland et al. 2000; (5) Peyronnet et al. 2007; (6) McCarthy et al. 2008; (7) Friedland et al. 2009a, (8) Russell et al. 2012; (9)Friedland et al. 2012a, (10) Friedland et al. 2003b, (11) Edwards and Richardson 2004, (12)Richardson and Schoeman 2004, (13) Ji et al. 2010

Table 2.2 - *Continued*

Causal Mechanism	Plausible Link	<i>northwest Atlantic Ocean</i>		<i>northeast Atlantic Ocean</i>	
		Evidence	Causal Certainty	Evidence	Causal Certainty
Altered ocean currents	Climate-altered ocean currents force salmon to expend more energy or shifts migration salmon to less favorable routes.	Altered currents observed (14,15) and effects on migration routes have been modelled (16). No field observations. Not assessed for repeat spawners.	HIGH (virgin) UNK (repeat)	Climate effect on currents observed (17,18). No field observations. Not assessed for repeat spawners.	MOD (virgin) UNK (repeat)
Climate impacts in FW	Warming climate has affected the size at smoltification, which leads to lowered survival given size-selective mortality.	Has largely decreased smolt age and size (19), which may impact survival, however no size-survival relationship identified. Not assessed for repeat spawners.	MOD (virgin) UNK (repeat)	Has largely decreased smolt age and size (19), which may impact survival, however size-survival relationship identified only in some regions (20,21,22,23). Not assessed for repeat spawners.	MOD (virgin) UNK (repeat)

Note: (14) Visbeck et al. 2003; (15) Drinkwater and Gilbert 2004; (16) Friedland et al. 2012b; (17) Edwards et al. 2001; (18) Dickson and Turrell 2000; (19) Russell et al. 2012; (20) Salminen et al. 1995; (21) Kallio-Nyberg et al. 2004; (22) Jokikokko et al. 2006; (23) Friedland et al. 2009b.

Table 2.3 - Potential causal mechanisms related to ecosystem regime shift and the associated trophic interactions that may have caused the observed shifts in salmon return rates and/or contributed to continued low return rates.

Causal Mechanism	Plausible Link	northwest Atlantic Ocean		northeast Atlantic Ocean	
		Evidence	Causal Certainty	Evidence	Causal Certainty
Effects of altered ecosystems					
ERS-altered prey abundance	Distribution / abundance of salmon prey reduces growth of salmon and subsequently survival.	Unlikely to impact postsmolt in NWA due to lack of growth-survival relationship (24,25,26,27). Effect on repeat spawners likely (28); requires further investigation. Prey species abundance has undergone major fluctuations (29,30,31,32).	LOW (postsmolts) HIGH (repeats)	Strong growth-mediated survival (24,33,34,35,36) makes bottom-up effects likely. Prey abundance has changed (37, 38). Observations of reduced growth noted (33,34). Repeat spawners unassessed.	VERY HIGH (postsmolts) UNK (repeats)
ERS-altered predator fields	Distribution / abundance, and behaviour of salmon predators leads to increased mortality	Abundance of many salmon predators has increased (39,40,41). Functional response of some predators does not favor salmon (42,43). Addition of new predators in some areas (44).	VERY HIGH (postsmolts) MOD (repeats)	Abundance of many important salmon predators variable (45,46,47). Functional response of predators unknown.	MOD (postsmolts) MOD (repeats)

Note: (24) Friedland et al. 2013; (25) Friedland et al. 2005, (26) Friedland et al 2009b; (27) Hogan and Friedland 2010; (28) Chaput and Benoit 2012; (29) Carscadden et al. 2001, (30) Choi et al. 2004, (31) Frank et al. 2005, (32) Bundy et al. 2009; (33) Friedland et al. 2000; (34) Peyronnet et al. 2007; (35) McCarthy et al. 2008; (36) Friedland et al. 2009a; (37)Beaugrand and Reid 2003; (38)

Beaugrand and Reid 2012; (39) Bowen et al. 2003; (40) Hammill et al. 2013; (41) Montevecchi et al. 2002;(42) Montevecchi 2007; (43) Rail and Chapdelaine 1998; (44) Friedland et al. 2012b; (45) Brander 2007; (46)Lonerger et al. 2007, (47) Thompson and Härkönen 2008.

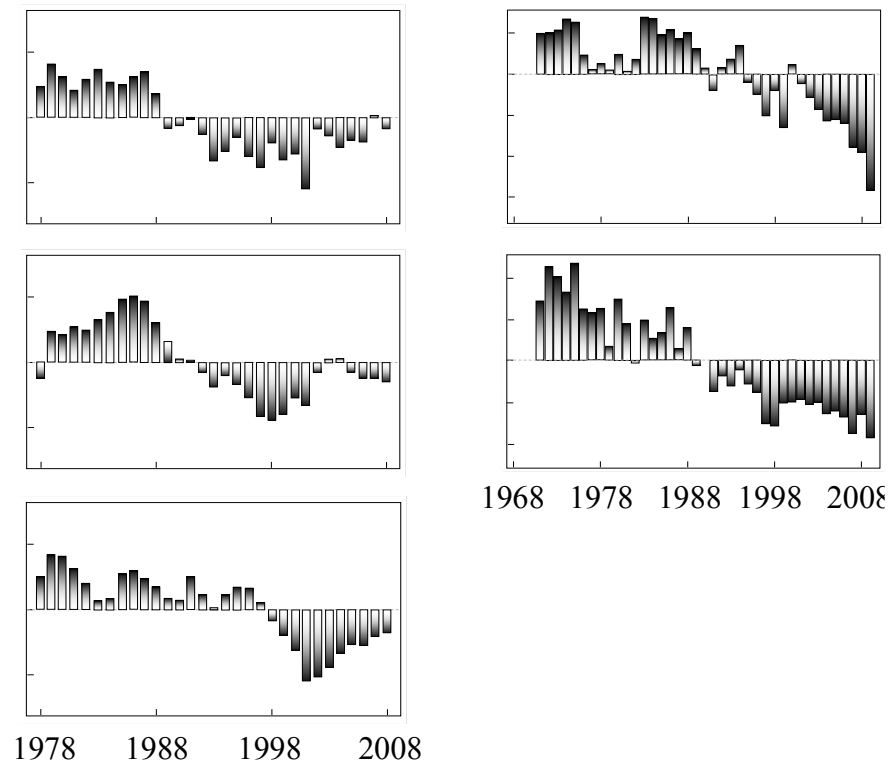


Figure 2.1 - Trends in Atlantic salmon marine productivity (y-axis) in the northwest Atlantic Ocean for the Scotia-Fundy (a), Gulf of St. Lawrence (b) and Labrador (c) regions and trends in the first principle component of prefishery abundance for maturing (d) and non-maturing 1SW (e) salmon in the northeast Atlantic Ocean. Figures adapted from Mills, K.E., Pershing, A.J., Sheehan, T.F. and Mountain, D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Glob. Chg. Biol.* 19: 3046–3061 (panels a-c) and from Beaugrand, G. and Reid, P. C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the northeast Atlantic. *ICES Journal of Marine Science* 69: 1549–1562 (panels d-e), by permission of Oxford University Press.

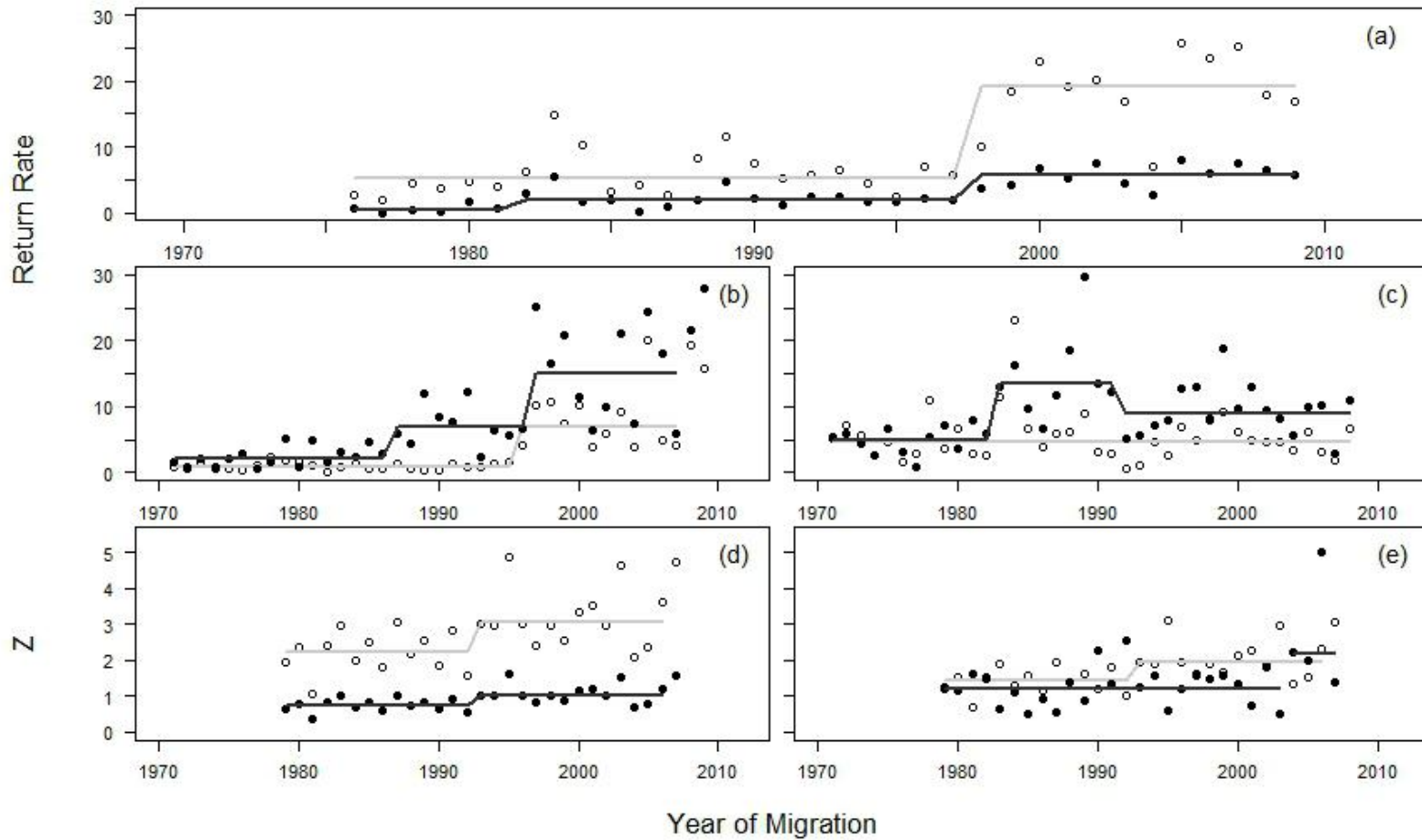


Figure 2.2 - Estimated survival of repeat spawning salmon. Return rates for female (open) and male (solid) salmon that first spawned as 1SW in the Teno River, Norway (a). Return rates for consecutive (b) and alternate (c) spawning salmon that first spawned as 1SW (open) and 2SW (solid) in the Miramichi River, New Brunswick, Canada. Estimated instantaneous mortality (Z) for salmon from the

Lahave River, Nova Scotia, Canada for male repeat spawners in their first year post-spawn (d) that first spawned as 2SW (solid) or 1SW (open), and (e) for female repeat spawners in their first year post-spawn (open) and all sexes and virgin sea ages during their second year at sea (solid). The grey (open) and black (solid) lines represent the weighed means based on the sequential t-test analysis of regime shift (Rodionov 2004) where changes in the mean signify statistically significant shifts in the mean (STARS, $l=7$, nominal p-value=0.10, actual p-value<0.01). Data used with permission from Niemelä et al. (2011), Chaput and Benoît (2012) and Hubley and Gibson (2011), respectively.

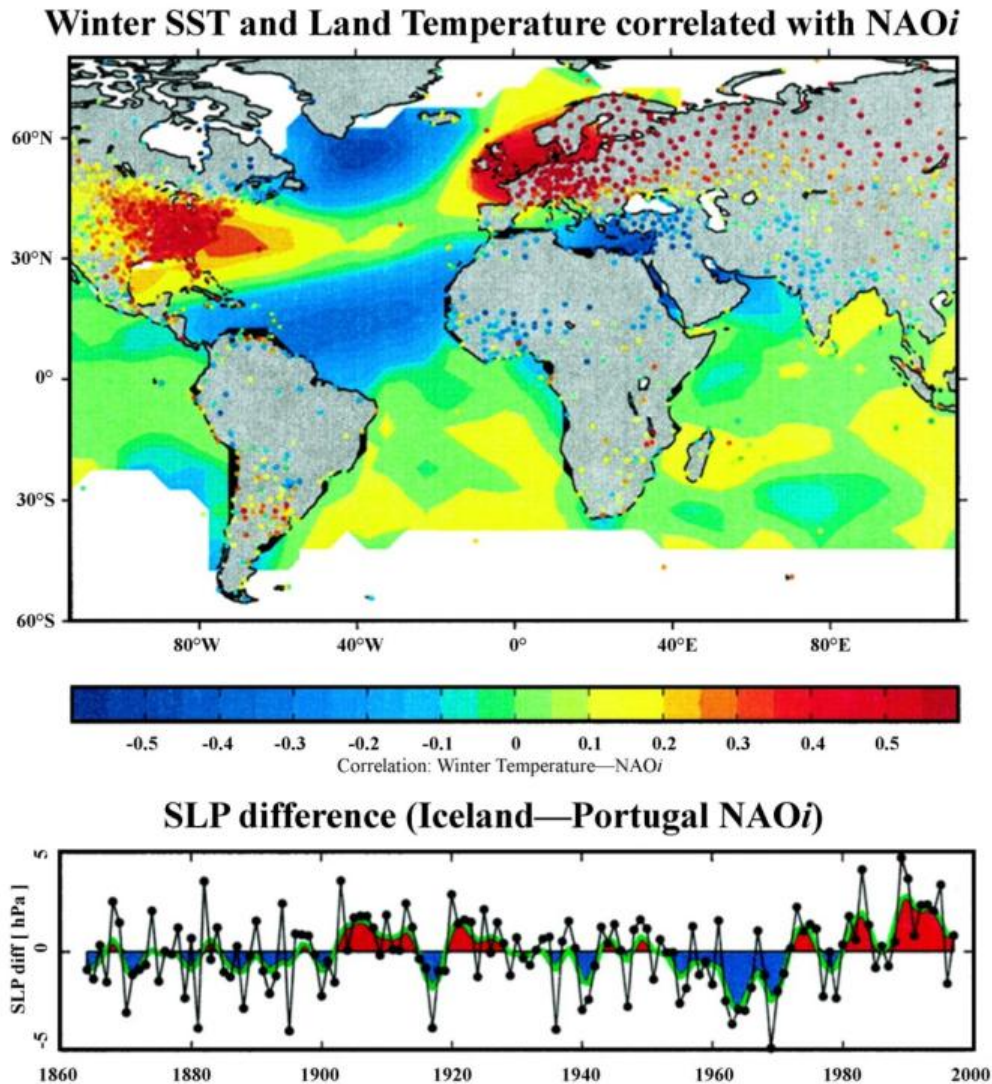


Figure 2.3 - Spatial correlation map of mean winter (DJFM) station temperature and sea surface temperature (SST) correlated against Hurrell's NAO index (Lower). During a positive NAO, colder conditions prevail over western Greenland and the Mediterranean region, whereas warmer conditions prevail in northern Europe, the northeast United States, and parts of Scandinavia. SST reflects a tripole pattern with a cold anomaly in the subpolar region, a warm anomaly in the mid-latitudes centred off Cape Hatteras, and a cold subtropical anomaly between the equator and 30°N. Copyright (2001) Highwire Press. Used with permission from: Visbeck, M.H., Hurrell, J.W., Polvani, L., and Cullen, H.M.(2001). The North Atlantic Oscillation: Past, present, and future. PNAS 98(23): 12876–12877. doi: 10.1073_pnas.231391598. Highwire Press.

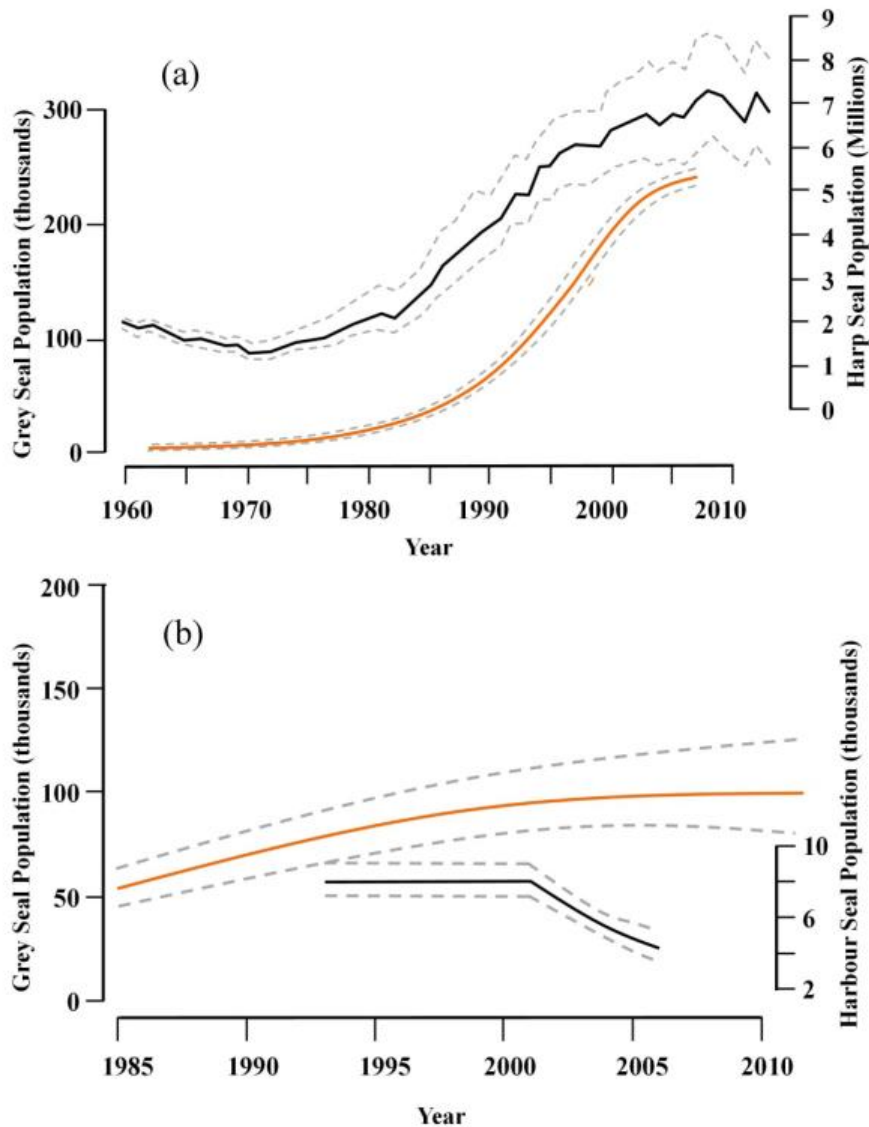


Figure 2.4 – Trends in seal abundance in the northwest Atlantic Ocean (A) and northeast Atlantic Ocean (B). Panel a: Estimated abundance of northwest Atlantic grey seals (solid orange line) and harp seals (solid black line), as modelled by Trzcinski et al. (2009) and Hammill et al. (2013), respectively. Panel b: Estimated abundance of grey seals in the UK (solid orange line) and harbour seals (solid black line) at the largest Harbour seal colony in Great Britain (Orkney), as modelled by Thomas (2013) and Lonergan et al. (2007), respectively. Grey dashed lines represent the 95% confidence intervals or credible

intervals, where relevant. Data used with permission in all cases, and with copyright permission from: Lonergan, M., Duck, C.D., Thompson, D., Mackey, B.L., Cunningham, L., and Boyd, I.L. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. *J. Zool.* 271: 261–269. John Wiley and Sons.

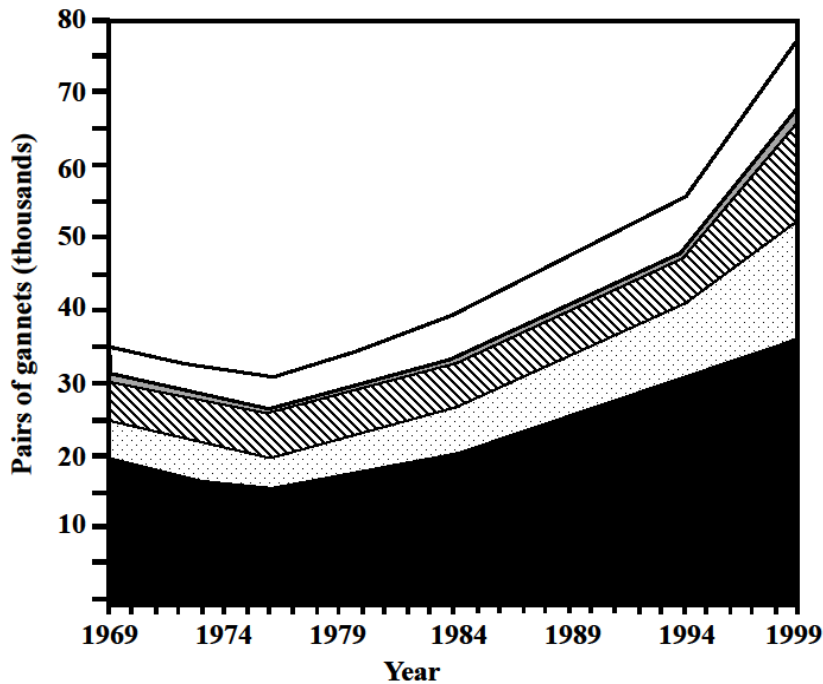


Figure 2.5 –Trends in breeding populations of northern gannets (*Morus bassanus*) in North America. Colonies (from top to bottom) are Funk Island, Nfld (open); Baccalieu Island, Nfld (light grey); Cape St. Mary's, Nfld (diagonal lines); Magdalen Islands, Quebec (dots); Bonaventure Island, NB (solid). Copyright (2002) National Research Council. Used with permission from: Monetevecchi, W.A., Cairns, D.K. and Myers, R.A. 2002. Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, National Research Press).

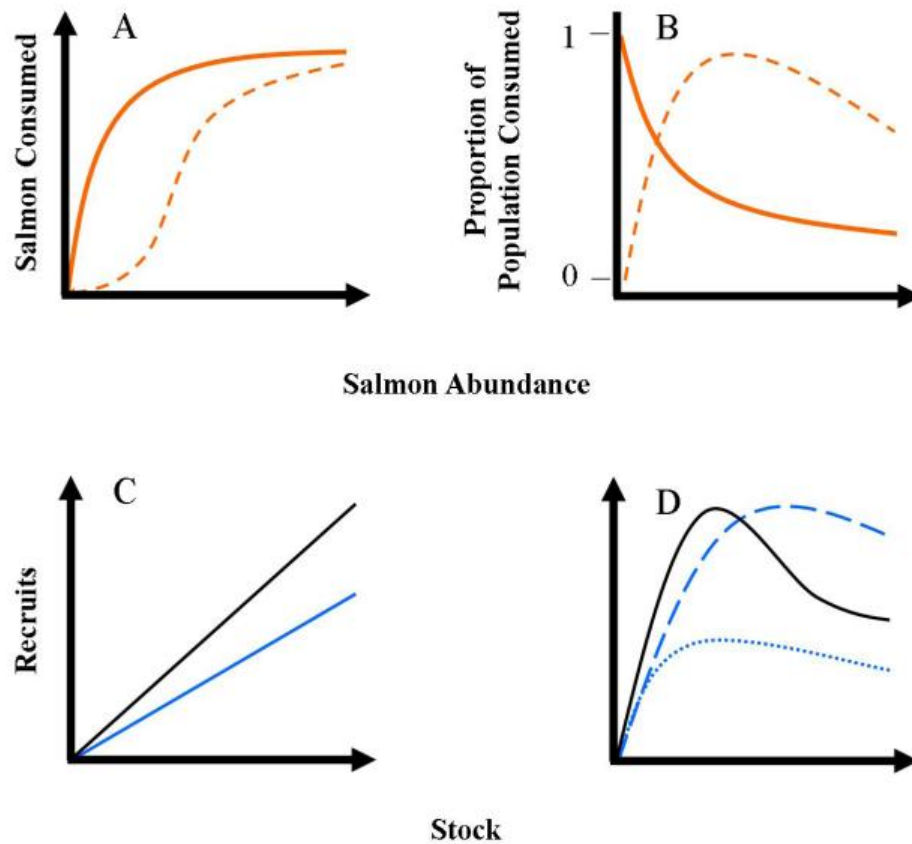


Figure 2.6 - Theoretical number of salmon consumed (A) and proportion of population consumed (B) when a predator exhibits a type II functional response (solid orange line) and a type III function response (dashed orange line). The effect of additive mortality (C) on a theoretical stock-recruitment relationship where mortality is either weakly or strongly density-dependant (solid blue line), or when there is no predation (solid black line). The effect of compensatory mortality (D) on a theoretical Ricker stock-recruitment relationship where mortality is either weakly (dotted blue line) or strongly density-dependant (dashed blue line), or when there is no predation (solid black line). Panels C and D adapted, with permission, from: Ward, D.M. and Hvidsten, N.A. (2011). Predation: Compensation and Context Dependence. pp. 199-220 in Aas, Ø., Einum, S.,

Klemetsen, A. and Skurdal, J. [Eds.]. Atlantic Salmon Ecology. Oxford. Wiley-Blackwell.

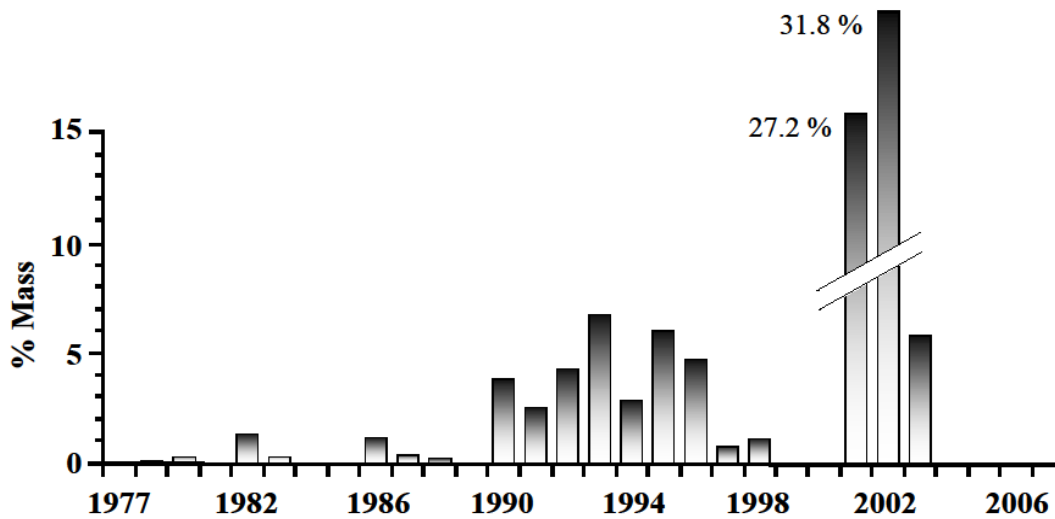


Figure 2.7 - Estimated percentages of total mass of northern gannet diets represented by Atlantic salmon landed in the northern gannet colony on Funk Island, Nfld, Canada from 1977 to 2006. Copyright (2007) Inter-Research. Used with permission from: Monetevecchi, W.A (2007). Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Marine Ecology Progress Series, Inter-Research.

**CHAPTER 3: ESTUARINE SURVIVAL AND MIGRATORY BEHAVIOUR OF
ATLANTIC SALMON SMOLTS FROM THE SOUTHERN UPLAND, NOVA
SCOTIA, CANADA**

Published as: Halfyard, E.A., Gibson, A.J.F., Ruzzante, D.E., Stokesbury, M.J.W., and Whoriskey, F.G. 2012. Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology* 81: 1626–1645. doi:10.1111/j.1095-8649.2012.03419.x

3.1. ABSTRACT

To estimate mortality rates, assess the spatio-temporal dynamics of natural mortality and examine migratory behaviour during the fresh- to saltwater transition, 185 wild Atlantic salmon *Salmo salar* smolts were implanted with coded acoustic transmitters. Seaward migration of tagged *S. salar* from four river systems in an area of Nova Scotia (Canada) known as the Southern Upland was monitored using fixed receivers and active telemetry over three years. Cumulative survival through the river, inner estuary, outer estuary and bay habitats averaged 59.6% (range 39.4 – 73.5%). When standardized to distance travelled, survival rates followed two patterns: (1) constant rates of survival independent of habitat or (2) low survival most frequently associated with inner estuary habitats. In rivers where survival was independent of habitat, residency periods were also independent of habitat, post-smolts exhibited few upstream movements, took a more direct route to the ocean and reached the ocean rapidly. Alternatively, in rivers where survival was habitat-specific, residency was also habitat-specific with overall increased residency, more frequent upstream movements and delayed arrival to the open ocean. The sudden ‘disappearance’ of most (75-100%) smolt / post-smolts assumed dead during the course of this study warrants further examination into the role of avian predators as a mortality vector.

3.2. INTRODUCTION

Atlantic salmon *Salmo salar* L.1758 populations of the northwest Atlantic Ocean have been in decline over the past two centuries (WWF, 2001), however a precipitous fall beginning in about 1990 (Hawkins, 2000, Potter et al. 2003) resulted in the extirpation of many populations, particularly those at the southern end of the distribution range (Parrish et al. 1998, COSEWIC, 2011). In Canada’s Maritime provinces, *S. salar* populations have also markedly declined (Gibson *et al.*, 2006), most notably in the Inner Bay of Fundy and Nova Scotia’s Southern Upland, both considered distinct designatable units by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). In the 65 rivers of the Southern Upland, many populations are extirpated and abundances in

remaining populations have declined by at least 75% since 1982, with most declining by > 90% (Amiro *et al.* 2000, Gibson *et al.* 2006). Identifying the causes of recent *S. salar* declines is difficult due to the species' plastic and anadromous life history. Within the Southern Upland, population declines are largely attributable to river acidification and reduced marine survival (Gibson *et al.* 2011).

Marine mortality of *S. salar* is hypothesized to be highest in the first few months of the migration (Hansen *et al.* 2003, Potter *et al.* 2003, Friedland *et al.* 2012), a period that includes post-smolts moving through estuarine habitats and entering the marine environment. Extreme ecological and physiological challenges are faced by *S. salar* in estuaries which are likely to contribute to mortality in this transitional zone (Hvidsten and Lund, 1988, Handeland *et al.* 1996, Dieperink *et al.* 2002). Ecological challenges facing *S. salar* in estuaries include predation and a niche shift. Fish and bird predation occurs on migrating salmonid post-smolts in estuarine environments (*e.g.* Hvidsten and Møkkelgjerd, 1987, Blackwell and Jaunes, 1998, Feltham and MacLean, 1996, Collis *et al.* 1998, Dieperink *et al.* 2002, Jepsen *et al.* 2006). Predation may intensify at migration constriction points (Blackwell and Jaunes, 1998) or at the head of tide, shortly after post-smolts first encounter salt water (Jarvi, 1989). Smolts also undergo major behavioural changes. In rivers as parr, *S. salar* are largely benthic, occupy relatively small home ranges and exhibit territorial behaviour, however, as smolt and post-smolt in the marine environment, *S. salar* shift to a pelagic existence, migrate across large spatial scales and relax territorial tendencies (Keenleyside and Yamamoto, 1962, Thorstad *et al.* 2011b).

In the estuary, smolts transition to post-smolts as they move from the hypotonic river environment to the hypertonic ocean environment, a transition that requires physiological adaptations such as increased size and abundance of chloride cells and elevated gill Na^+ , K^+ - ATPase activity (Folmar and Dickhoff, 1980, Hoar 1988). A failure to cope with seawater may lead to osmotic stress, and ultimately mortality, either directly or indirectly *via* reduced anti-predator behaviour and swimming performance (Jarvi, 1989, Handeland *et al.* 1996). As such, salmon smolt/post-smolt behaviour and survival may be driven by habitat-specific osmotic demands.

As a result of increased predation vulnerability, elevated physiological stress and behavioural transitioning, post-smolts in estuaries are expected to show habitat-specific adaptive changes in migration behaviour. The following hypotheses and predictions were addressed; 1) survival is habitat-specific and lowest within inner estuary habitats and 2) migration behaviour is habitat specific, with decreased swimming speed, and increased residency associated with the inner estuary. In this study, the migratory behaviour of *S. salar* smolts from Nova Scotia Southern Upland rivers was examined as they transited riverine, estuarine and coastal marine habitats. Survival rates were estimated with emphasis on documenting the timing and location of mortality.

3.3. METHODS

3.3.1. STUDY AREA

Salmo salar from four rivers along the Atlantic coast of Nova Scotia, Canada were studied, three rivers for a single year (2010) and one river for three years between 2008 and 2010. These rivers lie within the Southern Upland geological region, characterized by resilient (*i.e.* slow to degrade) bedrock and thin, poorly drained soils with low concentrations of base cations, lending surface waters susceptible to acidification (Kerekes et al. 1986). Study rivers (years sampled and approximate pH) were as follows, listed in order of decreasing pH (Watt *et al.* 2000): LaHave River (2010, pH > 5.4), St. Mary's River (2010, pH > 5.4), Gold River (2010, pH ~ 5.0 – 5.4) and West River, Sheet Harbour (2008-2010, pH ~ 4.7 – 5.0, Fig. 3.1). Drainage areas for the rivers were 1250, 1350, 370 and 282 km², respectively. Average mean annual flow (MAF) is 34.4, 43.0 and 11.0 m³ s⁻¹ for the LaHave, St. Mary's and Gold Rivers, respectively (Caissie 2000). Preliminary data suggests that MAF in the West River is approximately 8-9 m³ s⁻¹.

3.3.2. CAPTURE, TAGGING AND HANDLING OF SALMON

Wild *S. salar* smolts were captured as part of ongoing assessment processes at each study river, using rotary screw traps (E.G. Solutions Inc., Corvallis, Oregon, U.S.A.;

<http://home.teleport.com/~egs/>) and/or fyke nets (Gold, West and St. Mary's Rivers), angling (St. Mary's River), and a louvre deflection system (LaHave River). Once captured, *S. salar* smolts were held in 2 m diameter fiberglass streamside flow-through bins for 12 - 24 h prior to surgery. Individually-coded acoustic tags (v9-6L, 3.6 g in air, 9 x 24 mm, Amirix/Vemco, Halifax, NS, Canada; www.vemco.com) were implanted intraperitoneally following surgical procedures outlined by Chittenden *et al.* (2008). Post-surgery smolts were held in a streamside flow-through bin for 24 h to monitor immediate mortalities (four smolts in total from all sites died in this period). All surgical procedures were approved by the Dalhousie University Committee on Laboratory Animals (protocol #10-036).

Mean fork length (L_F) of tagged smolts from each river ranged from 16.9 to 20.3 cm and resulted in mean in-air tag-to-body mass tag ratios of 4.3 to 8.4 % (Table 3.1), generally within the suitable range for tagging salmonids. To minimize tag-induced mortality, recommendations for maximum tag-to-body mass ratio are < 8% for *S. salar* (Lacroix *et al.* 2004), <7% for Coho salmon *Oncorhynchus kisutch* (Walbaum, 1792) (Chittenden *et al.* 2009) and <6.7% for Chinook salmon *Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792) (Brown *et al.* 2010). Smolts were released between 1.6 and 53.3 km above head of tide (HoT), at their site of capture, with the exception of the St. Mary's River where the angled group was transported approximately 8.1 km upstream prior to release (Table 3.1).

3.3.3. PASSIVE AND ACTIVE MONITORING

Tagged *S. salar* were monitored *via* both passive monitoring and active tracking. Passive monitoring was achieved using omni-directional automated acoustic receivers (VR2 or VR2W, Vemco Ltd., Halifax, N.S., Canada) moored in fixed positions to a 3 m length of rope joining a float and anchor. The receiver was fastened to the riser *c.* 2 m above the anchor and *c.* 1 m below the float. Anchors were outfitted with a weighted drag line to aid in recovery. A total of nine to 23 receivers were deployed in each river/estuary (Table 3.1), covering each of the following four habitat zones; freshwater,

inner estuary, outer estuary and bay (Fig. 3.1). It is difficult to precisely delineate estuarine boundaries (*e.g.* Able 2005), and in this study, boundaries were roughly estimated based on; the location of HoT, channel width, benthic / sessile community structures and the influence of river-dominated currents. In general, salinities in the top *c.* 3 m of water were between 5-15 in the inner estuaries habitats, 10-22 in outer estuaries habitats and 20-28 in bay habitats. Tidal range in study areas was *c.* 1.0 – 2.5 m.

Smolts/ post-smolts were also actively tracked using a mobile receiver (Vemco model VR100) to improve accuracy of estimated positions and, at some sites, verify the presence of tags at the end of the study. Active tracking was done from a small boat by submerging an omnidirectional hydrophone for a minimum of 120 s at pre-determined stations (GPS coordinates) gridded 300 m apart. Additional stations were monitored as warranted by bathymetry (*i.e.* shallow shoals physically blocking signals) or high ambient acoustic ‘noise’ due to inclement weather, boat traffic or commercial operations.

To test detection efficiency of passive receivers and validate assumptions of effective detection range, 10 range-testing tags were moored among fixed receiver deployments. Detection efficiency incorporated both the probability of detecting a single transmission (using moored range testing tags at representative receiver spacing) and the probability of detecting a migrating smolt (Melnychuk 2009), which were generally >0.70 and >0.99, respectively. Other than a single receiver in the inner estuary of each the Gold River and Lahave River, *S. salar* smolt considered ‘surviving’ were detected on every receiver in succession as they migrated to sea (*i.e.* if a fish was detected on a receiver, it was also previously detected on all upstream receivers), indicating excellent system-wide detection efficiency. For this reason, detection efficiency was not included in survival estimates.

To estimate detection efficiency *via* active tracking, two tests were performed in 2010. First, detection efficiency was calculated as the proportion of tags known to be in the area *via* passive tracking data that were detected *via* active tracking. This assumes that detection probability was similar for tags in live smolts and tags in dead smolt or tags on the bottom due to fish mortality. Second, the cumulative probability of detecting a tag

(known to be present in the area) across all active tracking ‘searches’ was estimated. Active tracking was not conducted in the bay habitat zone in LaHave, Gold and St. Mary’s Rivers and the outer estuary habitat zone of the Gold River, primarily due to overly large areas or sustained inclement weather. During any given active tracking ‘search’, detection efficiency was high in the inner estuary and outer estuary habitats (mean = 88%, S.D. = 19%, range 50 - 100%), however efficiency decreased when searching bay habitats (mean = 58%, S.D. = 30%, range 36 - 93%). Consecutive (multiple) searches occurred for all actively-monitored habitat zones and increased the overall likelihood of tag detection to 95%. Detection probability in freshwater was not assessed.

At the West River in 2009, three receivers positioned 2.6, 10.2 and 10.3 km seaward respectively from the HoT, malfunctioned. Post-smolts with final detections immediately upstream from receivers positioned at 10.2 and 10.3 km from HoT ($n = 8$) were assumed to have survived and exited past the malfunctioning receivers. Coastal movements of *S. salar* post-smolts exiting the LaHave and Gold Rivers were monitored as tagged *S. salar* left these rivers and crossed a pre-existing line of acoustic receivers situated near Halifax, Nova Scotia (Ocean Tracking Network Halifax Line; Smith et al. 2009). At the time of this study, the line extended approximately 30 km perpendicular from the coast, with Vemco VR3 receivers bottom-moored every 800 m.

Fate of a tagged *S. salar* was determined from passive and active tracking records. During active tracking searches, some tags were repeatedly detected in the same location over multiple active tracking periods, and some tags not detected leaving the system via passive tracking were also not found in these surveys. In both cases, these tags were considered mortalities, and the latter were considered as ‘disappeared’.

3.3.4. DATA ANALYSES

All data were initially compiled in Vemco VUE software and analyses conducted in R 2.6.0 (R Development Core Team, 2009, Vienna, Austria, www.r-project.org/). Data

were sorted by river and year (*e.g.* LaHave River 2010, West River 2008, etc.), thus generating six river-year data sets.

Smolts that died within 1 km of their release site were considered casualties of the tagging procedure ($n = 7$) and were excluded from further analyses. Out-migration movements of *S. salar* smolts are not always unidirectional (*i.e.* seaward, *see* Kocik et al. 2009), thus to describe general patterns of movement, the number of changes in swimming direction were recorded for each individual, excluding movements of <1.6 km (2 x assumed detection range of 400 m radius for each receiver) to minimize potential issues of detection-range overlap and variable receiver spacing. Each change of swimming direction was assigned to the respective habitat zone the *S. salar* were in at the time. *Salmo salar* with no change of swimming direction were termed ‘unidirectional swimmers’. Swimming speed was expressed as body lengths per second (bl s^{-1}).

Residency was calculated as the sum of time spent within each habitat zone. To examine differences in residency, a two-way ANOVA model was fit to log-transformed residency data (standardized as days per km of zone length) and the categorical explanatory variables of river-year and habitat zone. Tukey’s Honest Significant Difference (HSD) was used for pairwise examination.

Tag expulsion (loss of tags through failed closure of sutures, *via* trans-coelom migration or *via* trans-intestinal migration) was not considered a significant issue in this study as the duration of tracking was generally less (mean = 21.9 days, S.D. = 11.2 days, max. = 47.8 days) than the reported onset of significant tag expulsion (Chisholm and Hubert 1985, Welch et al. 2007, Chittenden et al. 2009, Brown et al. 2010).

3.4. RESULTS

3.4.1. SURVIVAL

The rate at which smolts died enroute to the ocean varied among habitat zones and river-years. Cumulative survival to the open ocean / coastal zone for each river-year averaged 59.6% (S.D. = 13.3%) and ranged from 39.4 - 73.5% (Table 3.2). Trends in

mortality rates were examined after standardization for habitat length. In general, rates of survival followed two patterns; acute mortality in the inner estuary, as seen in Gold River and all years in the West River, or relatively consistent rates of mortality across all habitat zones in the remaining rivers (Table 3.2). Estimates of minimum survival are considered reliable, as detection efficiency of moored receivers was high. Detections of LaHave and Gold River post-smolts on the Halifax line of receivers provided minimum early ocean habitat-specific survival estimates of 23.5% (c. 70 km from bay Habitat) and 12.5% (c. 58 km from bay habitat), respectively, although some post-smolts are likely to have migrated past the outer terminus of the line.

To identify spatial areas and temporal periods of high mortality, the last known location of smolts/post-smolts assumed to have died prior to exiting the bay section of each river in each year of the study was analyzed. Of these *S. salar*, 34% were last detected within 1.9 km of the seaward side of the HoT (Fig. 3.2). Location of last detection relative to the HoT did not differ among river-years (Tukey HSD, d.f.= 43, all $P > 0.05$) with the exception of the LaHave River where distance from the HoT at last detection was significantly further upstream than occurred in all other river-years (Tukey HSD, d.f.= 43, all $P < 0.05$). After entering salt water, the mean time to last detection of post-smolts that died ranged from 2.6 - 18.2 days (Fig. 3.2 – LaHave River excluded due to low sample size). There was no difference in time to last detection in saltwater among river-years (Tukey HSD, d.f. = 34, all $P > 0.05$). Time to last detection in freshwater could not be calculated as sparse coverage by moored receivers introduced large spatial and temporal gaps.

Of the smolts/post-smolts that were deemed mortalities (based on fixed receivers), and occurred within areas monitored by active tracking, on average 86% failed to be located by subsequent active tracking (S.D. = 14%, range 63 - 100%, Fig. 3.3) and were considered to have ‘disappeared’.

3.4.3. MIGRATORY BEHAVIOUR

Swimming direction in freshwater was exclusively unidirectional (*i.e.* downstream), although receiver spacing in freshwater may not have recorded small-scale upstream movements. In the estuarine and marine environment, the proportion of post-smolts exhibiting unidirectional swimming across all river-years averaged 21% (S.D. = 16%, range = 8%–52%). Of the post-smolts which changed swimming direction, the average number of within river-year landward movements ranged from 1.75 to 5.94 (mean = 4.58, S.D. = 1.81). LaHave River (mean = 2.83) and St. Mary's River (mean = 1.75) post-smolts changed swimming direction less frequently compared to all other river-years (on average > 5 changes of swimming direction, Fig. 3.4). Most changes of swimming direction occurred in the outer estuary or bay in all river-years with the exception of Gold River, where 94% of all changes of swimming direction occurred within the inner estuary. The habitat-specific distribution of changes of swimming direction could not be assessed due to small sample sizes. Post-smolts most frequently used major channels or the largest opening seaward as the primary migration corridors. In the LaHave River, Gold River and West River 2009, where islands presented several exit pathways toward the open ocean, 96, 90 and 50%, respectively, of all post-smolts were detected exiting *via* the widest opening.

Residency (standardized by length of habitats) varied significantly by river-year (ANOVA, $F_{5, 467} = 30.9$, $P < 0.001$), by habitat zone (ANOVA, $F_{3, 467} = 71.3$, $P < 0.001$), and the interaction between river-year and habitat zone (ANOVA, $F_{15, 467} = 9.9$, $P < 0.001$). Post-hoc comparison revealed that the longest residencies in the Gold, West 2009 and West 2010 Rivers occurred in the inner and outer estuaries, with shorter residence times in freshwater and bay habitats (Table 3.3, Fig. 3.5). This pattern was not observed in other river-years, where residency generally did not differ significantly across habitat zones and was lower than other river-years (Table 3.3, Fig. 3.5). Small samples sizes at West River 2008 reduced statistical power. However, at this site, estimated residency over 3 years of observation was consistently longest in the inner estuary, with shorter residency in freshwater and bay habitats (Tukey HSD, d.f. = 467, all $P > 0.05$). Smolt travelled at various speeds and frequently in sinuous pathways,

incorporating multiple changes in swimming direction. Estimated mean ground speed, across all habitat zones and river-years, was 0.77 bl s^{-1} (S.D. = 0.77) and the 75th, 90th and 99th percentiles were 1.11, 1.86 and 3.50 bl s^{-1} , respectively. Mean migration speed for all habitat zones within a river-year was lowest in Gold River (mean \pm S.D. = $0.55 \pm 0.68 \text{ bl s}^{-1}$) and highest in St. Mary's River (mean \pm S.D. = $1.15 \pm 1.07 \text{ bl s}^{-1}$). With the exception of West River in 2008, migration speed was lowest in freshwater relative to other habitats, although this was only significant in West River 2010 (Tukey HSD, d.f. = 1681, $P < 0.01$), in West River 2008 and 2009 when compared to the bay (Tukey HSD, d.f. = 1681, $P < 0.05$ and $P < 0.001$) and in the LaHave River when compared to the inner estuary (Tukey HSD, d.f. = 1681, $P < 0.01$). After entering the estuarine environment, migration speed was not habitat-specific (Tukey HSD, d.f. = 1681, $P > 0.05$).

At least some *S. salar* post-smolts exiting the LaHave and Gold estuaries migrated north along the coast. Between 23 May and 3 June 2010, eight post-smolts of LaHave River origin and three post-smolts of Gold River origin were detected on the Halifax line which was 68 and 58 km north of the LaHave and Gold Rivers, respectively. Detections occurred at various points along the line, with a mean distance of 14.9 km from shore, (S.D. = 7.6 km, range 6.9 - 28.7 km). In the coastal habitat, post-smolts moved quickly to the Halifax line once they exited their estuaries, travelling on average at speeds of 1.53 bl s^{-1} (S.D. = 0.78). The average duration of detections as post-smolt crossed the Halifax array of receivers was 28 min 27 s (S.D. = 13 min 26 s), suggesting that smolts traversed the area rapidly. Most smolts travelled roughly parallel to the coastline (6 of 11), with some potentially angled seaward (4 of 11) and one potentially angled landward (1 of 11).

3.5. DISCUSSION

In this study, two distinct patterns of mortality and migration behaviour were identified among populations of *S. salar* from four rivers in Nova Scotia's Southern Upland. In rivers where mortality rates were high within the inner estuary, migratory behaviour was characterized by increased residency and more frequent upstream

movements. Alternatively, in rivers where mortality rates were similar among habitats, residency was instead shorter and similar among habitats and post-smolts made fewer upstream movements, passing more directly to the ocean.

3.5.1. *SURVIVAL*

The first study objective was to test the hypothesis that survival is habitat-specific and lowest within inner estuary habitats. Two basic mortality patterns were observed: evenly-distributed mortality across all habitats (LaHave and St. Mary's Rivers) and relatively acute and high mortality in the inner estuary (all other river-years). Noteworthy was the fact that periods of high mortality did not always result in poor overall survival to the open ocean (*e.g.* Gold River), as the duration of high mortality was not always sufficient to markedly reduce the numbers of tagged fish surviving. Overall survival estimates reported in this study (survival to the open ocean ranged from 39.4 - 73.5%) are within the range of previous studies from Eastern Canada and Europe. Lacroix et al. (2005) reported survival of 92 – 100% over 10 km for post-smolts in the Bay of Fundy, Canada. A subsequent study in the Bay of Fundy revealed significantly lower survival, ranging from 3 – 70% (Lacroix 2008), however these estimates encompassed a much larger spatial area and longer temporal period. In Norway's River Alta, *S. salar* smolt survival through the fjord was 75% (Davidsen et al. 2009).

Estimated mortality rates reported in this study are consistent with the suggestion that migration through estuaries is a period of particularly high mortality (Larsson, 1985). Further, these data support the hypothesis that marine mortality of *S. salar* is highest in the first few months at sea (Hansen and Quinn 1998, Hansen et al. 2003, Potter et al. 2003), as subsequent marine mortality rates must be lower than that observed in estuaries, considering normal overall marine return rates in this area are 1-5% (Gibson et al. 2009). Mortality within these habitats may also be important for *S. salar* at later life stages (Hubley and Gibson 2011). The impact of estuarine mortality on marine returns of adult *S. salar* is not well understood, and while speculated to significantly impact adult returns (Jepsen et al. 2006), this has yet to be empirically tested. Substantial mortality in the

estuary and subsequent high mortality in an open-ocean environment could additively reduce overall adult returns, and inter-population variability in marine mortality regimes may be influenced by mortality in estuarine and coastal areas specific to each population (Thorstad et al. 2007). If true, this study reports estuarine mortality ranging from 39.4 - 73.5 % among geographically-proximate rivers. This variability may be sufficient to account for, at least partially, variability in adult returns among neighbouring rivers. Furthermore, given that low smolt-to-spawner survival currently limits many populations, if survival in estuaries impacts marine returns, then conservation efforts can focus on improving estuarine survival to ultimately improve adult returns.

Alternatively, mortality in the open ocean may be the primary determinant of adult returns, with losses in estuaries having a minor effect of adult returns. For example, Friedland et al. (1993) found annual synchrony in marine return rates from five geographically dispersed *S. salar* populations, (latitudinal range = 41.3° N to 51.4° N) and surmised that the factors influencing marine returns acted on all populations simultaneously, presumably while they were in a common ocean environment. Similarly, Lacroix (2008) suggested that for *S. salar* post-smolts from the Bay of Fundy, factors outside the initial marine migration must be responsible for population declines.

Estimates of survival reported in this study hinge on the assumption that detections of tags represent the movements of live smolt. The potential of some tags being detected while in the stomach of piscivorous fishes / mammals cannot be ruled out, however, had predation occurred due to piscivorous fishes or marine animals, the acoustic tag would continue to send signals from the digestive track of these animals, and in many cases would provide specific and identifiable telemetry records that permit assignment of losses to specific predator types (Dieperink et al. 2002, Jepsen et al. 2006, Thorstad et al. 2007, Bendall and Moore 2008, Thorstad et al. 2011a).

Patterns in the location and timing of mortality, and particularly the frequency of tag ‘disappearance’ reported in this study indicate that predation by piscivorous birds are probably the most significant mortality vector. Interpreting the significance of a failure to detect a tag (*i.e.* a false negative) is problematic, and the confounding effects of failing to

detect a tag that was present cannot be ruled out. However, the high detection efficiency for both passive and active tracking experienced in this study (particularly the cumulative detection efficiency) suggests that failure to detect tags may in fact indicate that tags had not passed the receiver or were not in the area. Of all the tagged smolts not detected by fixed receivers, a large portion (75-100%) were also not detected subsequently via active tracking, a pattern consistent with what would be expected if tags were removed ('disappeared') from the water. Avian predators or scavengers are the most likely vector for removing tags from the water.

In typical 'disappearances', a smolt was detected exiting fresh water, arriving near the head of tide and subsequently 'disappearing' from passive and active monitoring. In one instance, a guano-covered tag was located nearly a month after it 'disappeared' from the study, 1m from a noted perching location for double crested cormorants *Phalacrocorax auritus* (Lesson, 1831). This suggests that the *S. salar* carrying it had been consumed by a *P. auritus*, transported to the perching location and the tag excreted. Should the remaining 41 cases of tag 'disappearance' (of 48 mortalities assessed for removals), also represent avian predation, then piscivorous birds would be a significant mortality vector for *S. salar* smolt / post-smolts. Stomach content analysis confirms that smolt constitute a possibly increasing portion of *P. auritus* diets in these study rivers (G. Randy Milton, *unpublished data*, Wildlife Division, Nova Scotia Department of Natural Resources, 136 Exhibition St., Kentville, Nova Scotia, Canada B4N 4E5, Milton *et al.* 2002). *Phalacrocorax auritus* abundance has increased in Nova Scotia since the 1920s (Milton *et al.* 2002) and *P. auritus* were the single most abundant predator in these study rivers in 2010, accounting for 50 % (mean, S.D. = 6%) of individual predators observed (E.A. Halfyard, *unpublished data*). Other avian predators present in the study areas included gulls (genus: *Larus*, mean proportion of predators = 18%, S.D. = 12%) loons, [*Gavia immer* (Brunnich, 1764), mean proportion of predators = 9%, S.D. = 7%], and mergansers (*Mergus serrator* L. 1758 and *Mergus merganser* L. 1758, mean proportion of predators = 9%, S.D. = 16%). Seals [*Phoca vitulina* L. 1758 and *Halichoerus grypus* (Fabricius, 1791)] were also observed, however at low abundance.

These analyses of tag ‘disappearance’ exemplify how additional information may be derived from acoustic telemetry projects, provided that project design incorporates sufficient active tracking, the study site(s) are amenable to active tracking, the efficiency of active tracking is assessed, and the limitations of data interpretation are discussed.

3.5.2. *MIGRATORY BEHAVIOUR*

The second study objective was to examine migratory behaviour of smolts/post-smolts in selected Nova Scotia Southern Upland Rivers, testing the hypothesis that migration behaviour was habitat specific, with decreased swimming speed, and increased residency associated with the inner estuary. Smolts exhibited two patterns of migration behaviours in contrast to what was expected. One was consistent with the hypothesis and showed habitat-specific behaviour, specifically residency (observed in Gold River and West River in 2008, 2009 and 2010). In the second pattern, found in the remaining two rivers, tagged *S. salar* had similar swimming speeds and residence times in different habitats. If differences in migration strategies affect survival and/or adult *S. salar* returns to rivers, then river-specific migration strategies may influence population viability at the river rather than the regional level.

Salmo salar post-smolts migrating through estuaries exhibited either rapid and unidirectional out-migration to the open ocean or, most commonly (79%), repeated seaward/landward movements prior to final out-migration. Changes of swimming direction have been reported by some authors as reflecting the behaviour of predatory fishes that have consumed a tagged smolt (Beland et al. 2001). This was not considered important in this study as: 1) tag tracks were screened for sustained high speed estimates (*i.e.* $> 4 \text{ bl s}^{-1}$) which are beyond the reported capabilities of smolts, 2) tags eventually out-migrated from study sites on dates similar to remaining tagged post-smolts and 3) populations of predatory fishes in the study areas are generally low.

Post-smolt migration through estuaries is primarily *via* active swimming (Lacroix and McCurdy 1996, Hedger et al. 2008) and post-smolts may change migration direction as a result of tidal influence or to maximize feeding opportunities (Hedger et al. 2008).

Repeated seaward/landward movements are prevalent in other rivers where acidification has occurred (Magee et al. 2001, Kocik et al. 2009). Similar movements have also been reported elsewhere (Moore et al. 1998, Hedger et al. 2008, Martin et al. 2009), although less prevalent and for shorter time periods. In the Southern Upland, post-smolts may make repeated changes in swimming direction as an acclimation strategy against variable osmotic-related stress associated with this environment.

While data presented in this study do not permit formal evaluation of the relationship between river pH and the prevalence of post-smolt reversal behaviour, post-smolts from the two rivers with the highest pH (LaHave and St. Mary's) exhibited only half as many reversals per individual than all other rivers-years and may suggest a negative relationship. A lack of seawater preparedness may alter estuarine behaviour of post-smolts (Magee et al. 2001, Strand et al. 2011) and seawater preparedness may be reduced, and osmotic stress amplified, for smolts previously exposed to freshwater acidification (Farmer et al. 1989, Staurnes et al. 1996, Kroglund and Finstad 2003). The impact of acidity on seawater tolerance, estuarine migration behaviour and overall marine survival may be an important phenomenon in Nova Scotia's Southern Upland given the region's widespread acidification (Watt 1997, Watt et al. 2000).

Estimates of residency also appeared to follow two primary patterns, homogeneous residency across all habitats (LaHave and St. Mary's Rivers), versus prolonged residency in the inner estuaries (all other river-years). Residency times in Southern Upland estuaries were generally greater than those reported for other eastern Canadian rivers (Lacroix et al. 2004, Martin et al. 2009). Extended residency at sites nearest the river mouth has also been reported from the non-acidified River Alta, Norway (Davidsen et al. 2009), although residency was shorter than reported in this study. Extended estuarine residency of smolts may indicate poor seawater preparedness (McCormick et al. 1985, Strand et al. 2011) and may represent an acclimation strategy.

Observations at the Halifax line of receivers provide some of the first insights on coastal migrations of *S. salar* smolts. Detections occurred between 6.9 and 28.7 km from

the coast, suggesting that few smolts were present in the less weather-exposed near-shore habitats and most had dispersed into offshore continental shelf waters.

Reduced marine survival is the suspected cause of population declines of *S. salar*, thus estimating the timing and location of mortality in the marine environment is important for future management considerations. Results of this paper highlighted the early migration period, and particularly inner estuary habitats, as locations/periods of particularly high mortality. Furthermore, patterns of mortality and tag ‘disappearance’ suggest that avian predation is a likely and significant mortality vector during this period. Further elucidation of factors contributing to early migration mortality and its influence on overall marine phase mortality is crucial to advancement of our knowledge of *S. salar* population regulation.

Table 3.1 - Summary of wild salmon smolts tagged with acoustic transmitters and released in Nova Scotia's Southern Upland.

Year	River	Number Tagged	Mean fork length (cm)(sd, range)	Mean tag-to-mass t ratio (%) (sd, range)	Release site (RKm)	Release as proportion of run	Receivers Deployed
2010	Gold River	35	18.7 (1.4, 17.0 - 22.5)	5.67 (1.07, 3.60-7.50)	1.6	0.45	n=23
2010	LaHave River	35	19.7 (1.7, 17.4-23.7)	5.15 (1.25, 3.21-7.25)	25.1	0.23	n=15
2010	St. Mary's River	35	16.9 (0.8, 15.5-18.3)	8.36 (1.24, 6.00-11.25)	8.7 (17), 53.3 (18)	0.78	n=9
2008	West River (Sheet Harbour)	19	20.3 (1.0, 18.4-22.2)	4.29 (0.62, 3.26-5.63)	7.6	0.60	n=15
2009	West River (Sheet Harbour)	26	19.1 (1.1, 17.9-21.6)	5.42 (0.88, 3.53-6.67)	6.9	0.15	n=15
2010	West River (Sheet Harbour)	35	19.5 (1.7, 17.4-25.0)	5.29 (1.27, 2.37-7.50)	6.9	0.32	n=16

Note: Tag-to-mass ratio is the tag mass in air divided by the mass of the smolt in air, expressed as percent. Release site is the distance upstream from the head of tide (River Km). Numbers in parentheses next to release site is the number released at each site (if more than one release site). Release as proportion of run indicates the fraction of the cumulative salmon smolt catch at traps on each river at the time that tagged smolt were released. For river-years with multiple release dates, the sum of cumulative proportions weighted by the proportion of total tags released on each date is reflected. Cumulative catch data was river-year specific, with the exception of Gold River where 2011 data were used and St. Mary's River where 2008 data were used as a proxy.

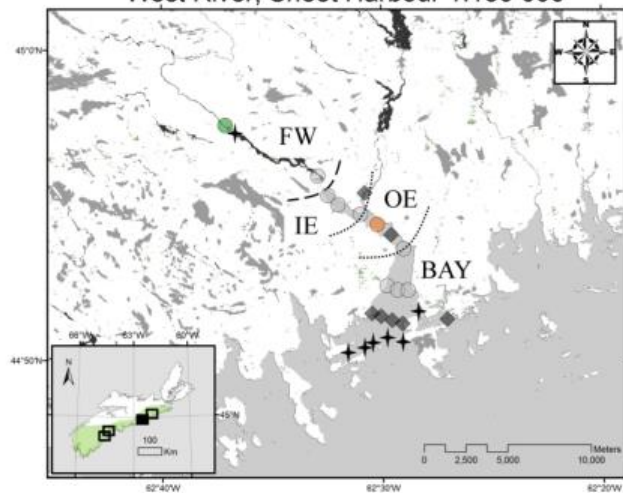
Table 3.2 - Observed cumulative survival (%) and standardized survival (% per km of habitat zone length) of smolts upon exit from the four habitat-zones.

River-Year	Observed Cumulative Survival Upon Exit			
	FW	IE	OE	BAY / Overall
LaHave	76.5% 98.9% · km ⁻¹	76.5% 100.0% · km ⁻¹	73.5% 99.7% · km ⁻¹	73.5% 100.00% · km ⁻¹
Gold	100.0% 100.0% · km ⁻¹	88.2% 92.4% · km ⁻¹	79.4% 97.8% · km ⁻¹	61.8% 97.6% · km ⁻¹
St. Mary's	79.4% 99.3% · km ⁻¹	76.5% 98.7% · km ⁻¹	73.5% 98.7% · km ⁻¹	67.6% 98.3% · km ⁻¹
West 2008	78.9% 97.0% · km ⁻¹	52.6% 83.8% · km ⁻¹	47.4% 96.5% · km ⁻¹	47.4% 100.0% · km ⁻¹
West 2009	96.0% 99.5% · km ⁻¹	76.0% 90.5% · km ⁻¹	72.0% 98.3% · km ⁻¹	68.0% 98.8% · km ⁻¹
West 2010	71.9% 95.5% · km ⁻¹	54.5% 91.0% · km ⁻¹	51.5% 98.0% · km ⁻¹	39.4% 95.0% · km ⁻¹

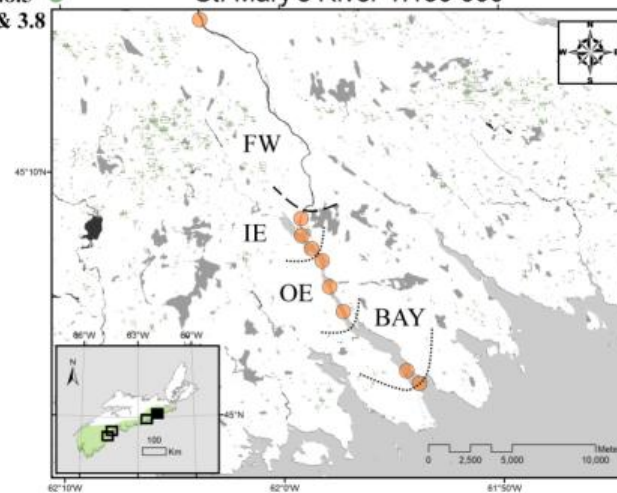
Note: Smolt tags detected stationary within one km of the release site were excluded from estimates of observed survival. FW = Freshwater, IE = Inner Estuary, OE = Outer Estuary and BAY = Bay habitats

Note: Explanatory variables tested were river-year and habitat zone. Significance codes are as follows: non-significant (-), $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Cross-hatched cells are replications of comparisons depicted elsewhere in the table or comparisons of little logical interest (i.e. only comparisons of habitats within a river-year or between river-years for a given habitat were of interest). FW = Freshwater, IE = Inner Estuary, OE = Outer Estuary and BAY = Bay.

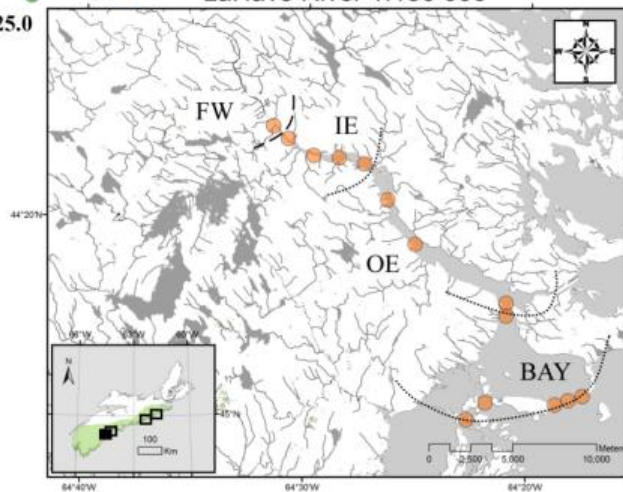
West River, Sheet Harbour 1:150 000



48.5
& 3.8 St. Mary's River 1:150 000



25.0 16.8 LaHave River 1:150 000



Gold River 1:150 000

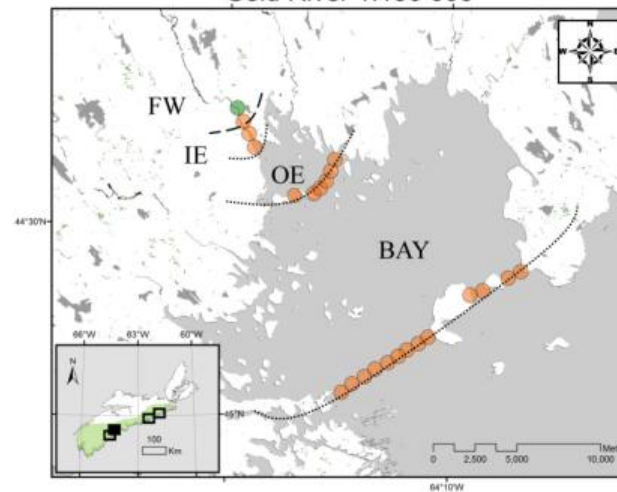


Figure 3.1 - Map of study area for the four study watersheds: (a) West River, Sheet Harbour, (b) St Mary's River, (c) LaHave River and (d) Gold River, indicating tagged smolt release (●) and receiver locations. Receiver locations icons represent deployments in: any river, 2010 only (●), West River, Sheet Harbour 2008–2010 (●), West River, Sheet Harbour 2009–2010 (◆) and West River, Sheet Harbour 2008 only (✦). The inset map in each of the four panels provides an outline of Nova Scotia, with the green outline depicting the approximate area of the Southern Upland; ■, the study area; □, all remaining study areas. In the LaHave and St Mary's Rivers, tagged smolt release and some receiver locations were outside the mapping area, thus their distance (km) from the upstream bound of the mapping area is indicated adjacent to the icon.

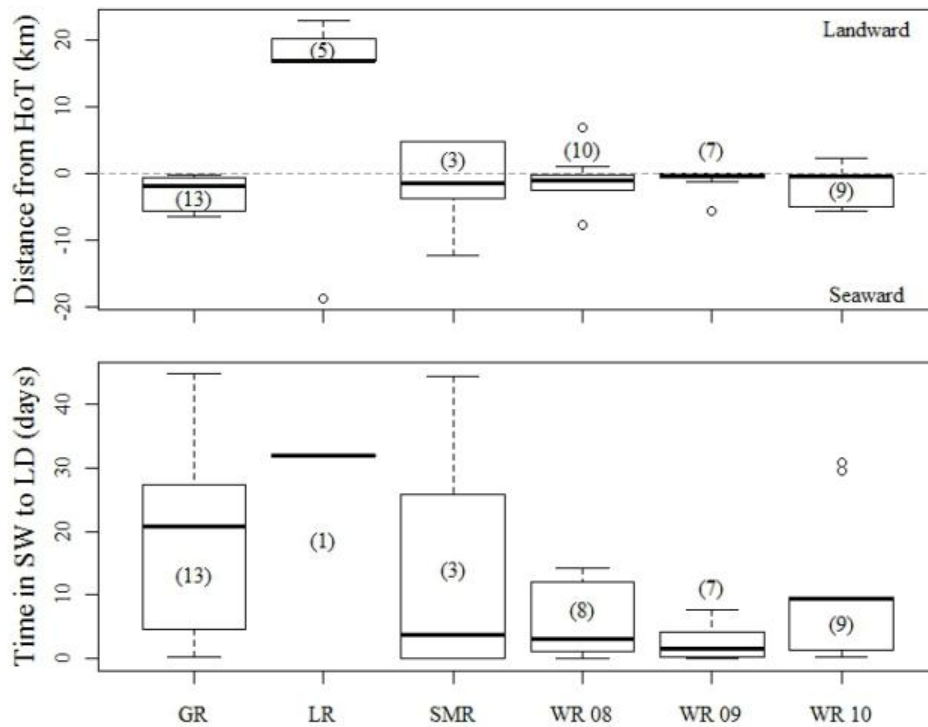


Figure 3.2 - Location and timing of last detection (mortality) for all river-years. (a) Distance to last detection relative to head-of-tide (HoT). Positive numbers represent the landward side of HoT and negative number the seaward side of HoT. (b) Time after saltwater entry (SW) to last detection (LD). Sample sizes are shown in parentheses. LH, LaHave River; GO, Gold River; SM, St Mary's River; W08; West River 2008; W09, West River 2009; W10, West River 2010. Release locations (distance above HoT) were as follows: LH = 25.0 km, GO = 1.9 km, SM = 8.7 or 53.3 km, W08 = 7.5 km, W09 = 6.8 km and W10 = 6.8 km. Box plots represent median (solid black line), interquartile range (extremities of box) and 5th and 95th percentiles (whiskers).

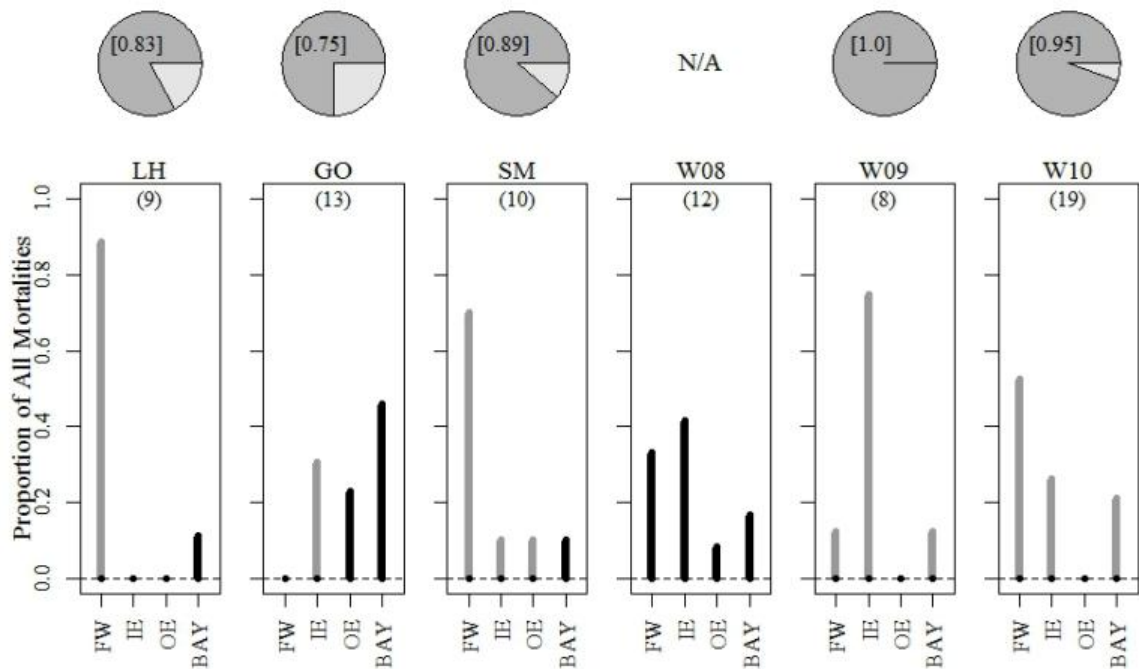


Figure 3.3 - Proportion of all mortalities (estimated from passive tracking) occurring within each habitat zone. Sample size in parentheses represents sum of all losses within each river-year. ■, habitat zones examined *via* active tracking; ■, zones where active tracking did not occur. Pie charts indicate the proportion of all mortalities for which the tags were not found *via* active tracking (*i.e.* disappeared). LH, LaHave River; GO, Gold River; SM, St Mary's River; W08, West River 2008; W09, West River 2009; W10, West River 2010; FW, fresh water; IE, inner estuary; OE, outer estuary; BAY, bay habitats; N/A, not applicable.

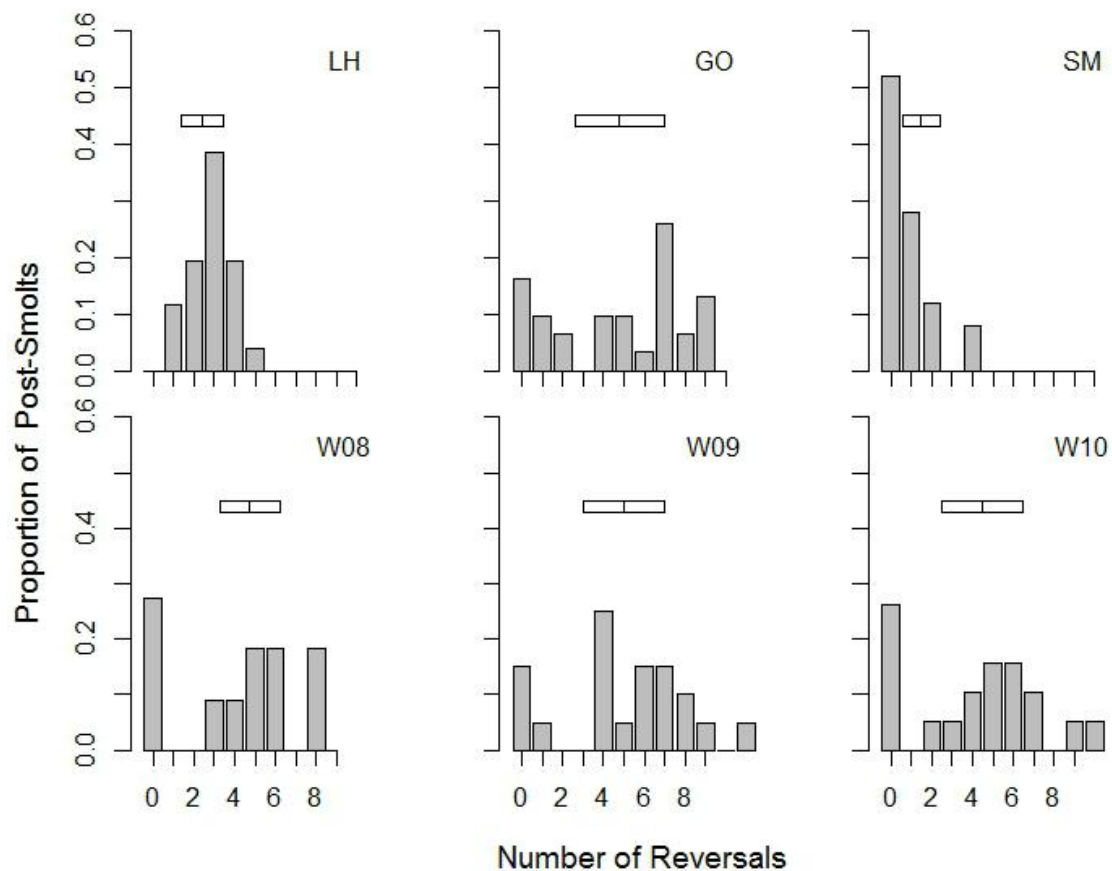


Figure 3.4 - Histograms of the proportion of smolts (all river-years) exhibiting changes of swimming direction. Unidirectional swimming is represented by zero changes in swimming direction in (a) LaHave River, (b) Gold River, (c) St Mary's River, (d) West River 2008, (e) West River 2009 and (f) West River 2010. Their location on the x -axis indicates the number of regressions for those excluded smolts. , mean \pm s.d. number of changes of swimming direction.

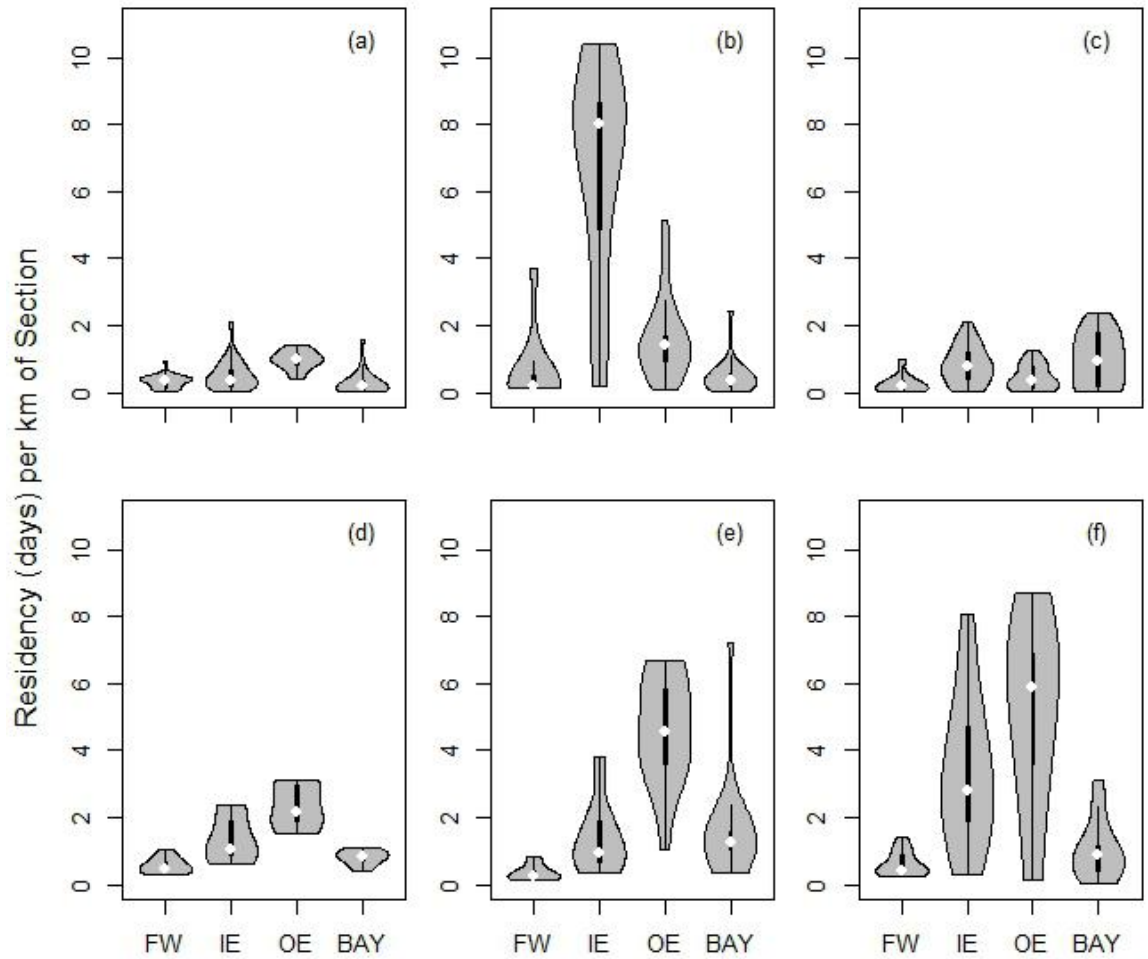


Figure 3.5 - Violin plots of residency for each habitat zone within each of the six river-years and among habitat zones for (a) LaHave River, (b) Gold River, (c) St Mary's River, (d) West River 2008, (e) West River 2009 and (f) West River 2010. Only smolts deemed to have survived were included in the plot. Shape of the plots is from locally weighted density of the data, estimated by kernel method. The boxplot within each violin plot indicates the following: median (○), 25th and 75th percentile of data (extremities of thick black line). FW, fresh water; IE, inner estuary; OE, outer estuary; BAY, bay habitats.

**CHAPTER 4: CORRELATES OF ESTUARINE SURVIVAL OF ATLANTIC
SALMON POSTSMOLTS FROM THE SOUTHERN UPLAND, NOVA SCOTIA,
CANADA**

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4.1. ABSTRACT

Acoustic telemetry is a useful tool to monitor the estuarine survival and behaviour of Atlantic salmon postsmolts. Most frequently, survival is reported as the static fraction of tagged postsmolts detected, and while the timing or location of mortality may be reported, covariates of survival or the relationship between migratory behaviour and survival are less often described. In this study, we used acoustic telemetry to follow Atlantic salmon smolts migrating to sea from four rivers in Nova Scotia, Canada. Further, we tested the relationship between migratory behaviour and survival and used mark-recapture models to examine the role of body length and tag-to-body weight as survival covariates. Survival was most heavily impacted in estuarine habitats closest to head-of-tide. Survival was affected by body length at three of four sites. The shape and spatial variability of the body length-survival relationship provided insight on mortality vectors, highlighting the potential roles of predation and osmotic stress. Survival was not influenced by repeated landward/seaward migratory movements; however, there was a significant correlation between residency and survival.

4.2. INTRODUCTION

Atlantic salmon (*Salmo salar* L.) populations within the southern portion of their North American range have declined dramatically (Parrish et al. 1998; WWF 2001; COSEWIC 2011), due in large part to reduced marine survival (Lacroix 2008; Gibson et al. 2009; Gibson et al. 2011). Deriving empirical estimates of short-term (e.g. weeks to months) marine mortality for this species is difficult. Using acoustic telemetry, researchers have estimated mortality rates during the estuarine migration, which is the transition point from riverine to marine habitats, the place the fish spend their first few weeks in the ocean, and a place and time where previous studies have reported intense mortality (Kocik et al. 2009; Davidsen et al. 2009; Halfyard et al. 2012). Causes of estuarine losses may include predation (e.g. Hvidsen and Møkkelgjerd 1987; Hvidsten and Lund 1988; Dieperink et al. 2002), osmotic stress (Staurnes et al. 1996; McCormick et al. 1998), and/or their interaction (Järvi 1989; Handeland et al. 1996).

Acoustic telemetry provides data that allow the reliable estimation of fish movement and migration. Unfortunately, such estimates are rarely linked with assessments (either qualitative or quantitative) of mortality vectors. More recently, however, Atlantic salmon data derived from acoustic telemetry have been analyzed via mark-recapture modelling (Kocik et al. 2009; Lacroix 2008; Davidsen et al. 2009). This approach allows the formal evaluation of survival covariates at the population and/or individual levels as well as the evaluation of telemetry gear performance (specifically the probability of detecting tagged fish) by providing confidence bands around survival estimates. Covariates and the spatio-temporal patterns of covariate strength may provide insights into mortality vectors if those covariates have an adaptive ecological function (e.g. the effects of fish size on susceptibility to predation). Mortality vectors can also be examined by linking survival with behaviour. In response to physiological stress, physical stress, or predation pressure, fish may alter their behaviour in unique and predictable ways (Sigismondi and Weber 1988; Mesa 1994; Olla et al. 1995) which may ultimately influence survival.

Predation in estuaries is likely high. Constricted spaces, such as estuaries, concentrate predators and likely increase predator-prey encounters (Brown and Mate 1983; Blackwell and Jaunes 1998; Zamon 2001). Within estuaries, postsmolts faced with osmotic stress may have difficulty adjusting to the marine environment (McCormick et al. 1985) and could alter migratory behaviour by increasing residency while acclimating. Postsmolts may also make multiple, short seaward/landward movements (termed “reversals”, *see* Kocik et al. 2009), returning to the less physiologically-demanding hyposaline river plume for short periods should the osmotic stress of the estuarine environment temporarily overwhelm their developing osmoregulatory capacity (Magee et al. 2001; Kocik et al. 2009). Postsmolts under stress, and exhibiting increased residency or a higher frequency of reversals, would increase their exposure to predators which should ultimately decrease survival. In addition to stress-related differences in mortality rates, there are likely size-based advantages with larger individuals more successfully avoiding predation (e.g. Werner and Gilliam 1984; Blaxter 1986; Miller et al. 1988)

In this study we observed Atlantic salmon smolts migrating to sea from four rivers in Nova Scotia, Canada and examined the potential factors that influenced mortality by using mark-recapture modelling. We explored the relationships of a number of covariates with survival, and examined the influence of migratory behaviour on survival. We tested two predictions regarding estuarine migration and mortality. First, smolt size was predicted to show a strong positive correlation with survival, with the strength of this correlation likely varying among rivers and habitats. Second, survival was predicted to correlate with migratory behaviour, specifically residency (i.e. time spent migrating) and migration strategy, where increased residency and the prevalence of repeated seaward/landward movements would be negatively correlated with survival. Identification of survival correlates may highlight important mortality vectors of Atlantic salmon postsmolts in estuaries- a crucial step for future salmon conservation.

4.3. METHODS

4.3.1. OVERVIEW

Acoustic telemetry was used to evaluate the survival and migratory behaviour of wild Atlantic salmon smolts from four rivers in Nova Scotia, Canada (Fig. 4.1). These rivers lie in the Southern Upland, a geological region severely affected by anthropogenic acidification (Watt et al. 1983, Watt et al. 2000). Year of tagging and sample size for each of the four study rivers in order of increasing mean ambient river pH were: West River, Sheet Harbour (2008; N = 19, 2009; N = 26, 2010; N = 30), Gold River (2010; N = 30), LaHave River (2010; N = 30), and St. Mary's River (2010; N = 30), for a total of six river-years of data. Salmon smolts were captured in their respective rivers using various traps, surgically implanted with an acoustic transmitter (v9-1L, Amirix/Vemco, Halifax, NS, Canada), held in a flow-through, streamside tank and released at the site of capture the day following surgery. Surgical procedures were approved by the Dalhousie University Committee on Laboratory Animals (protocol number 10-036).

Acoustic receivers were deployed to passively monitor the downstream movements of smolts, delineating four distinct habitats in each river drainage; freshwater

(i.e. river), inner estuary, outer estuary and bay (Fig. 4.1). Receivers were mounted approximately 1-3m above bottom. Active tracking was also periodically conducted, where a mobile receiver was soaked for >120 s at pre-determined GPS co-ordinates gridded 300 m apart. In areas where bathymetry or high turbulence was suspected to decrease detection efficiency, additional stations were monitored as required. Further details regarding surgical, equipment and procedural methodologies are given in Halfyard et al. (2012).

4.3.2. *MARK-RECAPTURE MODELLING*

To assign the fate of individual smolts, we interpolated movements from passive and active tracking data. Analysis of mortality was conducted assuming that mortality had occurred when: a) a tagged smolt ceased movement over an extended period of time, b) a tagged smolt was not detected leaving the study area by the end of the study, or c) a tagged smolt was not detected leaving a monitored area, and subsequent active tracking in that entire area failed to detect the tag.

For a smolt to be detected on a receiver, the smolt must a) survive to reach the receiver, and b) be detected by the receiver. As such, both survival (S) and detection efficiency (p) must be considered when discussing survival (White and Burnham 1999). Because salmon smolts ultimately move from the river to the ocean in a unidirectional manner, and are bounded by land on two sides, we used passive receivers as our sampling ‘events’. The distance between two passive receivers was considered the sampling interval for which survival was estimated. Consequently, models estimated survival for each passive receiver interval along the progression of smolt migration. Survival estimates were standardized by the length of the receiver interval (i.e. survival per km). Only detections during the final seaward migration for each smolt were used, and all previous seaward movements (i.e. if the postsmolts exhibited reversals) were ignored.

Two approaches were used to model survival. First, in river-years where the observed detection efficiency was less than 100% at one or more receiver locations (LaHave and Gold Rivers), both the apparent survival and the detection efficiency were

estimated using Cormack-Jolly-Seber models (CJS, Cormack 1964; Jolly 1965; Seber 1965). All CJS models were tested for goodness-of-fit (i.e. over-dispersion) using a bootstrapping method with $n=1000$ simulations. The estimated quasi-likelihood, over-dispersion parameter (\hat{c}) was <1.0 in all models, and thus no adjustments were made (Burnham and Anderson 2002). Secondly, in river-years where detection efficiency was 100% at all receiver locations (West River 2008, 2009, 2010 and St. Mary's River), survival was estimated using known-fate models (White and Burnham 1999). Detection efficiency was considered to be 100% when detections of tagged smolts were preceded by one or more detections on all upstream receivers. Known-fate models assume a detection efficiency of 1.0 and estimate survival only, but avoid the confounding effects of unknown detection efficiency. Goodness-of-fit could not be assessed for known-fate models.

Modelling was conducted using the program MARK (White and Burnham 1999). For both classes of models, fork length (L_F) and tag-to-body weight ratio (TWR) were included as covariates after being z-transformed to increase comparability among populations where covariates significantly differed (e.g. L_F). TWR was included as a method of accounting for potential tag-burden effects, although it is somewhat confounded with L_F , as body weight is positively correlated with L_F and thus longer smolts had a lower TWR. We ignored potential growth during the study and assumed that L_F and weight measured at the time of tagging was representative of the fish for the duration of tracking (mean = 26 days). A pool of nested models was derived from a set of general starting models (i.e. global models). All models used the logit link function. Models were ranked based on Akaike Information Criterion (AIC) scores and calculated AIC weights. AIC addresses issues of balance between under- and over-fit models and formally weighs model bias and variance trade-offs (Burnham and Anderson 2004). Because several models showed utility in describing the data, parameter estimates were derived via weighted model averaging (Johnson and Omland 2004), encompassing the uncertainty of all suitable models within a river-year. Tagged smolts that failed to register on any receiver and for which active tracking confirmed a stationary location within 1 km

of the release site (n=8) were assumed to have died as a result of the tagging procedure and were removed from the survival analysis.

4.3.3. *STATISTICAL ANALYSES OF BEHAVIOURAL CORRELATES*

Salmon postsmolts in the estuary exhibited either unidirectional swimming behaviour (i.e. direct to the ocean), or one or more seaward-landward reversals of swimming direction prior to their final seaward exit. Because some smolts died prior to exhibiting reversals, it was not known whether they would have performed reversals if they had lived. If we consider a) reversal behaviour, and b) death without reversal behaviour as the two possible ‘events’ (i.e. outcomes), then these events can be considered ‘in competition’ as death without reversal behaviour precludes observation of future reversal behaviour. As such, competing risk analysis (Pintilie 2006) was used to estimate the cumulative incidence function (i.e. cumulative probability of exhibiting reversals) prior to the time of death for each individual dying without reversals (i.e. unidirectional migration only). This estimate was subtracted from the asymptotic estimate of the proportion of smolts exhibiting reversals (i.e. the maximum probability that a smolt would show reversals), to reveal the probability that a particular smolt would have eventually exhibited reversals if it had survived. Differences between observed versus expected frequencies, for the pooled dataset, were examined using the G-test (Sokal and Rohlf 1995).

Survival of salmon smolts may be impacted by the time spent in estuarine habitats. To test the relationship between survival and residency, we fit generalized linear models (GLMs) to the fate of individual postsmolts (dependant variable) with a binomial distributed error structure (logit link function). Standardized (days·km⁻¹) overall (all habitats) residency times was the continuous explanatory variable. Because of significant collinearity between river-years and residency, river-year could not be included as a categorical explanatory parameter (Quinn and Keough 2002). Preliminary analysis revealed that overall residency was significantly different among river-years (One-way ANOVA, df = 5, $F_{5, 148} = 26.5$, $p < 0.001$), and post-hoc analysis using Tukeys HSD, at $\alpha =$

0.05 suggested three river-year groupings of overall residency; 1) the LaHave and St. Mary's Rivers, 2) the Gold River and West River 2010, and 3) the West River 2008 and 2009. As such, GLMs were fit to the data for each grouping respectively. Goodness-of-fit was assessed for all final GLMs following the decile method of Hosmer and Lemeshow (1980; 1991).

4.4. RESULTS

Using ten moored range-testing tags, we were able to validate our assumptions of effective detection range and estimate detection efficiency of passive receivers. The probability of detecting a single transmission was generally >0.70 , while the probability of detecting a migrating salmon smolt was >0.99 . Active tracking efficiency was also tested during the entire length of the study. During any given active tracking 'search', the likelihood of detecting a tagged postsmolt (if present) was $88 \pm 19\%$ (mean \pm s.d.) in inner and outer estuary habitats, however efficiency dropped to $58 \pm 30\%$ (mean \pm s.d.) in bay habitats. In any given river-year, the probability of detecting a tagged postsmolt (if present), at least once, during active tracking was approximately 95%.

4.4.1. INFLUENCE OF BODY SIZE ON SURVIVAL

Mark-recapture modelling suggested that survival differed among habitats, with support for habitat-specific survival in four of six datasets (Gold, West 2008, 2009, and 2010). There was insufficient support for habitat-specific survival in the remaining two datasets (Fig. 4.2, Tables B.1-B.6), which were best described by constant rates of survival (Fig. 4.2, Table B.5, Table B.6). In cases where habitat-specific survival was supported, survival was always lowest in habitats immediately seaward of head-of-tide (i.e. the inner estuary).

The inclusion of L_F (or TWR which is roughly inversely proportional to L_F) as a covariate significantly improved the explanatory power of the models for all datasets except the St. Mary's River (Tables B.1-B.6). Covariates did not influence survival

consistently among datasets (Fig. 4.3). In most river-years where survival was habitat-specific, so too was the shape and slope of the survival-covariate relationship. In the West River 2010 where survival was habitat-specific, the nature of the L_F -survival relationship was constant among habitats. In the LaHave River, where survival was constant, there was support for the inclusion of L_F as a survival covariate, however, this was independent of habitat (i.e. constant among habitats). The minimal adequate model of St. Mary's River did not include L_F as a covariate, however, there was support for the inclusion of release location. The St. Mary's River was the only river where two distinct release locations were used.

4.4.2. INFLUENCE OF BEHAVIOUR ON SURVIVAL

During their seaward migration, salmon smolts that exhibited reversals did so between 0.1 and 26.7 days after entering the estuarine environment (mean = 6.4, sd = 5.6), while salmon smolts that died without reversals did so between <1 to 13.9 days (mean = 3.9, sd = 4.3) after entering the estuary (Fig. 4.4). The majority of smolts (79%) exhibited one or more reversals and the average number of reversals per smolt was 4.6 (Halfyard et al. 2012). Results of the competing risk analysis indicated that the likelihood a salmon smolt that died would have performed one or more reversals if it had lived, ranged from 0.04 to 0.77, with a mean likelihood of 0.53 (95% CI, 0.48 – 0.58, Fig. 4.4). We used the mean estimates of the probability that a smolt would have performed reversals, if it had not died, to calculate the true proportion of postsmolts performing reversals. In this analysis we found insufficient support (G-Test, d.f. = 1, $p = 0.109$) for the hypothesis that survival was influenced by migration strategy (i.e. those moving straight to the ocean vs. those performing repeated reversals). However, using the estimates at the lowermost bound of the 95% CI for the likelihood a salmon smolt that died would have performed one or more reversals, if it had lived, a slight survival advantage was observed, where smolts not exhibiting reversals were more likely to survive (G-Test, d.f. = 1, $p = 0.047$).

Standardized overall residency was a significant predictor of survival for smolts from the Gold River and West River 2010 group and from the West River 2008 and 2009

group, but not for smolts from the LaHave River and St. Mary's River (Table 4.1). The model for Gold River + West River 2010 appeared to fit the data adequately, however there evidence of significant lack of fit for the West River 2008 and 2009 model (Table 4.2). There was support for inclusion of a quadratic residency term in the model for Gold River and West River 2010 (Table 4.1), where survival was predicted to increase with increasing residency between values of approx. $0\text{--}2\text{ days}\cdot\text{km}^{-1}$, decreasing thereafter (Fig. 4.5).

4.5. DISCUSSION

This study described the timing, location and magnitude of mortality for Atlantic salmon smolts and postsmolts and examined the impact of behaviour and body length on survival. The nature of survival-covariate relationships, their habitat- or site-specific variation and the nature of behaviour-survival correlations allowed us to identify potential mortality vectors for salmon. The examination of survival-correlates may add additional value to telemetry studies and provide important insight to potential mechanisms underlying observations of mortality.

4.5.1. *INFLUENCE OF BODY SIZE ON SURVIVAL*

Mortality rates were specific to both rivers and habitats, with some rivers experiencing low mortality that was consistent among habitats while others experienced relatively high mortality that was variable depending on habitat. For the latter, habitats immediately downstream of the head-of-tide exhibited the highest mortality (*see also* Halfyard et al. 2012). Where survival was habitat-specific, those habitats with high mortality (i.e. the inner estuary) were presumably locations of severe selective pressures such as high predator densities or high physiological demand. Survival rates reported in this study, standardized to the length of habitat, were often greater than $0.90\cdot\text{km}^{-1}$, however by the time that smolts reached the open ocean, total survival averaged only 59.6% (range = 39.4–73.5%, *see* Halfyard et al. 2012). Survival rates appear intense as significant losses occur over short spatial scales (particularly for the inner estuaries of

Gold and West Rivers), however mortality rates through the remainder of habitats and estuaries are not particularly high relative to subsequent mortality that must occur in the open ocean to produce the return rates of 1-5% observed in nearby index rivers (*see* Gibson et al. 2009).

The shape of the survival-covariate relationship may provide insight on potential mortality vectors. For example the positive-correlation between L_F and survival in the LaHave and Gold Rivers typifies what would be expected if predation intensity is high. Smolts may experience increased survival if they are larger than the preferred prey size of predators, or as a result of improved predator avoidance with size. In general, survival and the ability of fish to avoid predators increases with size (*see review by* Sogard 1997). In the rivers examined for this study, Double Crested Cormorants *Phalacrocorax auritus* (Lesson) were found to be the most abundant predator (E.A. Halfyard, *unpublished data*) and have been reported to be significant predators of salmon smolts as they migrate to sea (Blackwell et al. 1997; Cairns 1998; Milton et al. 2002). While cormorants can prey upon the entire range of observed L_F for salmon smolts in this study area, they may select smolts from the smaller end of the length-frequency range (Hatch and Weseloh 1999), potentially accounting for the size-dependant survival observed in this study. Smolts in West River (all years) also experienced size selective survival however, unlike those from LaHave and Gold Rivers, survival favoured smaller individuals. Following optimal foraging theory (e.g. Pyke 1984), larger smolts should be preferred provided the increased calories they provide are not offset by increased capture costs. Negative size-survival correlations have been previously described for fish under controlled conditions (Litvak and Leggett 1992; Pepin et al. 1992; Rice et al. 1993), and in the field, particularly with regard to bird predators (Britton and Moser 1982; Trexler et al. 1994). However, all of these studies have examined young-of-year or very small juveniles (< 8 cm). Evidence of size-selective mortality favoring smaller individuals for fish of comparable length to salmon smolts is lacking. Larger (and presumably older) smolts from the West River may be predisposed to poor seawater performance such as impaired osmoregulation, and thus low survival, due to anthropogenic stress such as river acidification (Saunders et al. 1983; Magee et al. 2003), although this study does not

provide evidence to test this theory. As such, this study cannot definitively identify the functional mechanism behind this trend for postsmolts.

Tag weight was held constant in this study, thus TWR is approximately inversely proportional to L_F , and both of these survival-covariates could represent tagging-induced mortality. However, tagging induced mortality was considered low for this study because TWR was within a range conducive to high survival (Lacroix et al. 2004; Chittenden et al. 2009; Brown et al. 2010). Furthermore, the negative survival – L_F correlation observed in the West River cannot be attributed to tagging-induced mortality.

Spatial trends of the impact of covariates and their strength, both habitat-specific and among-river, may also provide insight toward mortality vectors. Among-habitat variability in the shape of the L_F -survival relationship highlights those habitats where selective pressures are most intense. In our dataset, the inner estuary of the Gold River and West River in 2008 and 2009 exhibited the most extreme covariate-survival relationship. In the inner estuary, high concentrations of smolt predators may account for the extreme size-selected survival. Predators have been reported to favour the area around head-of-tide or at constriction points within estuaries during the smolt run (Hvidsten and Lund 1988; Dieperink et al. 2002; Jepsen et al. 2006). Salmon are first exposed to saltwater in the inner estuary and mortality may occur as a result of osmotic stress or an associated reduction in predator avoidance ability (Järvi 1989; Handeland et al. 1996). Body size, particularly the disproportionate increase of volume to surface area, may be an important determinate of a smolts ability to deal with osmotic stress (Parry 1960; Muir 1969). As a result, larger individuals should possess an osmoregulatory advantage over smaller smolts, which should also produce a survival advantage

At a larger scale, variability in physical, chemical, ecological and oceanographic attributes of rivers and their estuaries may influence salmon smolt behaviour and ultimately survival (Lacroix 2008; Plantalech Manel-La et al. 2011). The positive L_F -survival correlation observed in the LaHave and Gold Rivers, the negative L_F -survival correlation observed in all three years at the West River and the lack of significant survival covariates in the St. Mary's River suggest that even within Nova Scotia's

Southern Upland, major among-river differences exist and may contribute to the relative success of each of these populations. Estuaries with gradual and extensive mixing zones may facilitate increased survival by reducing osmotic stress or by providing a larger area for smolts to occupy during their transition, thus minimizing predator constriction points. Understanding the estuary-specific features conducive to survival may suggest management strategies to improve survival.

4.5.2. INFLUENCE OF BEHAVIOUR ON SURVIVAL

The behavioural response of an individual Atlantic salmon smolt faced with a new environment, new predators, and new physiological demands may ultimately influence its survival. This study identified a significant quadratic (humped) relationship between survival and residency for smolts from the Gold River and West River 2010, a non-significant relationship for smolts in the West River in 2008 and 2009 and no support for a relationship in either the LaHave or St. Mary's Rivers. Following the classification of Watt et al. (2000), the Gold and West River are the most acidic, with a mean pH between 4.7 and 5.4, while the LaHave and St. Mary's River have a mean pH > 5.4, which is above a level expected to severely impact salmon populations in this region. Although this study was not designed to test effect of river pH on subsequent postsmolt survival, and there was minimal replication of study sites (2 acidified – 2 less acidified), the division of significant relationships among rivers that differ in pH warrants further consideration. A survival-residency relationship may reflect a behavioural response to physiological status and seawater tolerance (Tytler et al. 1978; McCormick et al. 1985; Kroglund and Finstad 2003). Exposure to acidic conditions reduced the seawater tolerance of smolts, and those ill-prepared for the transition to seawater exhibit high levels of stress and reduced survival (Staurnes et al. 1996; Kroglund and Finstad 2003; Kroglund et al. 2007). Further, physiological stress may induce lethargy in fish (Sangalang et al. 1990; McCormick and Jensen 1992; Beyers et al. 1999), and smolts have been shown to delay sea-entry if they are osmotically ill-prepared (Strand et al. 2011). It therefore stands to reason that altered migratory behaviour would extend into the estuary in an attempt to mitigate poor seawater tolerance.

Our findings of a humped relationship between survival and residency differ from those of Dempson et al. (2011) who reported a positive residency-survival relationship. Both the positive phase of the humped relationship presented in this study, and that of Dempson et al. would be expected if increased residency in the estuary promotes survival by slowing the rate of transition from freshwater to saltwater and decreasing stress related to osmoregulation. However, the negative second quadratic term shown in Fig. 4.5 likely describes an alternative mechanism, most probably predation-related mortality. Because predation pressure in estuaries is high (Hvidsten and Møkkelgjerd 1987; Dieperink et al. 2002; Jepsen et al. 2006), a negative relationship may reflect the effect of increased exposure to predation.

Reversal behaviour may also reflect a behavioural response to increasing salinity and the associated osmotic stress, which may be exasperated by previous exposure to acidic conditions (Magee et al. 2001; Kocik et al. 2009). Our results suggest that survival was not influenced by reversal behaviour, and as such, fails to support the theory that reversals are related to physiological condition. Alternatively, given the considerable literature suggesting that survival is influenced by acid-induced stress (e.g. Staurnes 1996; Kroglund and Finstad; Kroglund et al. 2007), then should reversals be unrelated to acid stress (i.e. reversals are ubiquitous among postsmolts regardless of acid-induced stress level), our results would suggest reversal behaviour does not improve survivorship for postsmolts under stress. Previous studies reporting reversal behaviour have focused on both acidified rivers (Magee et al. 2001; Kocik et al. 2009; Halfyard et al. 2012) and non-acidified rivers (Martin et al. 2009; Dempson et al. 2011), and therefore support alternative theories regarding the mechanism behind reversal behaviour. This study does not examine plausible alternative explanations. Reversals may also represent acclimation to temperature gradients (Dempson et al. 2011), although this has been poorly tested.

Our finding of no survival cost or benefit associated with reversal behaviour differed from the findings of Kocik et al. (2009) who concluded that smolts performing repeated reversals experienced higher survival than those following a unidirectional path to the ocean, although this was not assessed statistically. One potentially confounding effect when analyzing such data is the relationship between survival longevity and the

opportunity to perform reversals (i.e. smolts that died without having exhibited reversals may have, in fact, exhibited reversals had they survived). In this study, we attempted to address this potentially confounding issue using competing risks theory, where it was assumed that the likelihood of exhibiting migration reversals was similar for all salmon smolts / postsmolts in the population.

Our results support the theory that mortality of Atlantic salmon postsmolts in estuaries is high across short spatial scales, spatially variable, and is likely related to predation, osmotic stress or predation-osmotic stress synergies. Further, our results highlight the need for river-specific identification of factors contributing to mortality. Given the potential link between estuarine behaviour, physiological status and estuarine survival, further investigation that includes comprehensive bioassays of physiological status may be important for understanding behavioural differences among smolts and the implication for future conservation planning.

Table 4.1 - Logits of parameter (β) and standard error (SE) estimates for generalized linear models with binomial error distributions, fitted to binary fate data (0 = died, 1 = survived) and the explanatory variable of standardized overall residency (SOR).

Models and Terms	β Estimate	SE	z-value	Pr > z
LaHave + SMR				
SOR	-1.490	1.241	-1.201	0.230
Gold + West 2010				
SOR	6.100	1.924	3.171	0.002
SOR ²	-1.618	0.495	-3.273	0.001
West 2008 + 2009				
SOR	4.003	1.258	3.181	0.001

Table 4.2 – Diagnostic results of generalized linear models, with binomial error distributions, for each of the three river-year groupings

River-Year	Model Terms	Null Deviance	Residual Deviance	Deviance Explained	Residual d.f. (Null d.f.)	<i>Goodness-of-Fit</i>		
						\hat{c}	d.f.	p-value
LaHave + SMR	Fate ~ SOR	49.72	48.30	2.86%	55 (56)	17.48	8	0.025
Gold + West 2010	Fate ~ SOR + SOR ²	75.04	56.06	25.29%	53 (55)	11.91	8	0.155
West 2008 + 2009	Fate ~ SOR	55.64	33.72	39.40%	39 (40)	25.72	8	0.001

Note: Dependant data were binary fate (0 = died, 1 = survived) and the explanatory variable was of standardized overall residency (SOR), expressed as (days·km⁻¹), and the square of SOR. Goodness-of-fit (GoF) calculated using the Hosmer-Lemeshow decile test (Hosmer and Lemeshow 1980; 1991). GoF p-values < 0.05 indicate significant lack of fit..

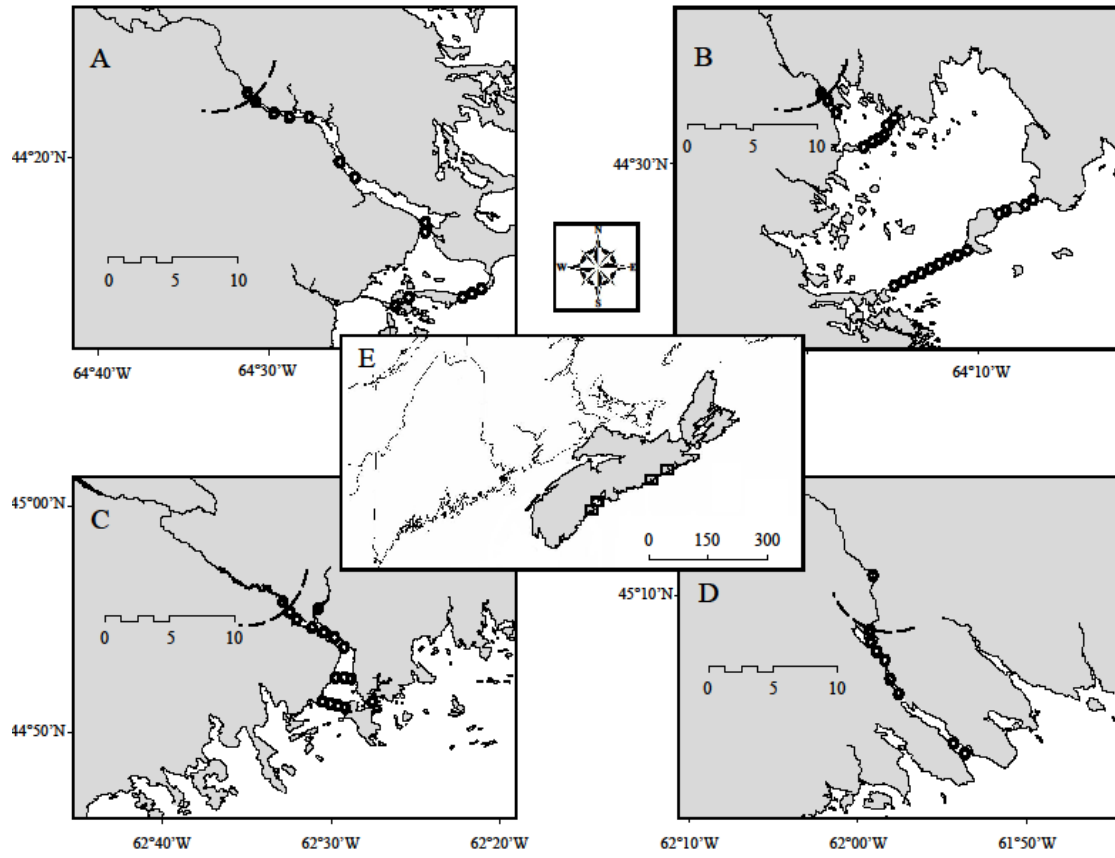


Figure 4.1 - Maps of the following study areas, from southwest to northeast: (A) Lahave River, (B) Gold River, (C) West River, Sheet Harbour, (D) St Mary's River, and (E) their relative locations (black boxes) within Nova Scotia. The location of all 2010 receivers (O) and approximate location of the head of tide (dashed line) are shown for each study site. For the location of West River, Sheet Harbour receiver locations in 2008 and 2009, or for addition information, please refer to Halfyard et al. (2012).

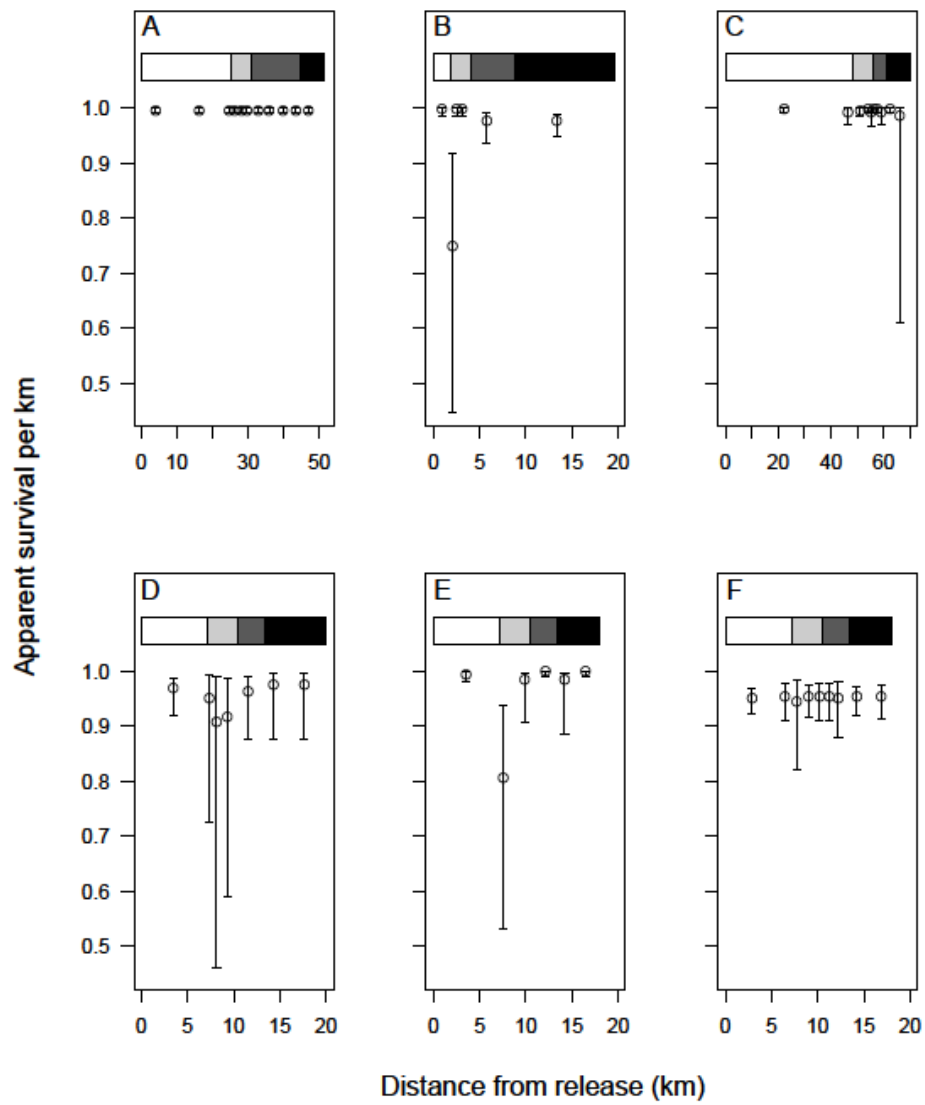


Figure 4.2 - Estimates (95% CI) of apparent survival for each river-year, at each receiver interval, as a function of distance from release in the Lahave River (A), Gold River (B), St. Mary's River (C), West River 2008 (D), 2009 (E), and 2010 (F). Estimates were derived from model averaging the pool of Cormack-Jolly-Seber models (Lahave and

Gold) and known-fate models (St. Mary's, West 2008-2010). For St. Mary's River survival estimates, points represent only the upper release location. Bars along the top of each plot represent the delineation of the following habitats as a function of distance from release site: white = freshwater (river), light grey = inner estuary, dark grey = outer estuary and black = bay.

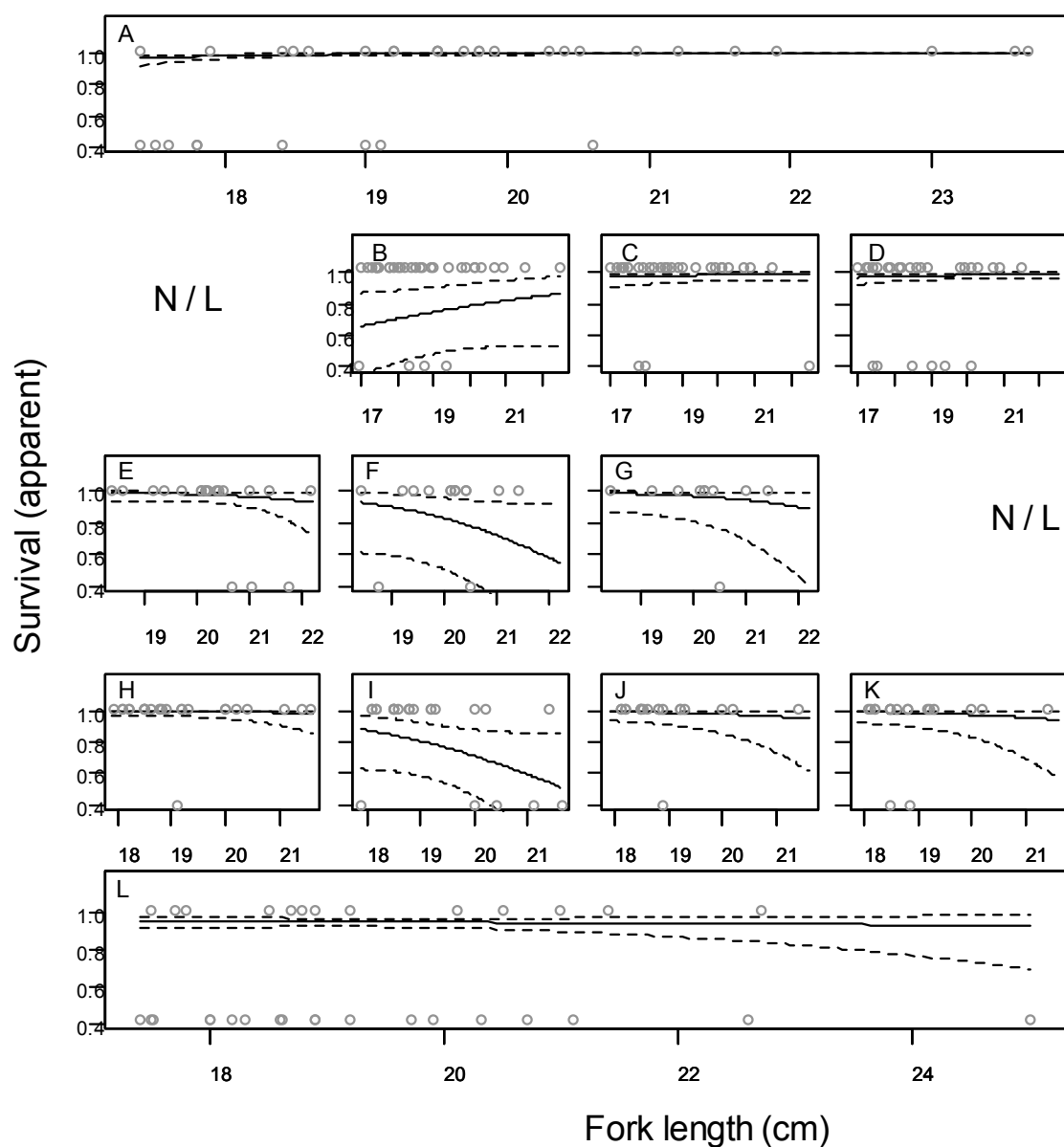


Figure 4.3 - Plots of covariate (fork length - cm) effects on apparent survival per km.

Dark solid lines represent the estimated regression line, and dashed lines represent the upper and lower 95% confidence intervals. Open grey circles represent the fork length and fate of each individual smolt used in the covariate models, with circles at the top and bottom of each plot representing smolts that survived and died, respectively. Columns represent the following habitat zones (from left to right); Freshwater, Inner Estuary,

Outer Estuary and Bay. River-years were as follows: Lahave River – all habitats zones (A), Gold River, inner estuary (B), Gold River, outer estuary (C), Gold River, bay (D), West River 2008, freshwater (E), West River 2008, inner estuary (F), West River 2008, outer estuary (G), West River 2009, freshwater (H), West River 2009, inner estuary (I), West River 2009, outer estuary (J), West River 2009, bay (K), and West River 2010, all habitats zones(L). Missing plots represent no-losses (N / L) during that river-year / habitat zone. The St. Mary's River is not represented as there was no evidence of a covariate effect.

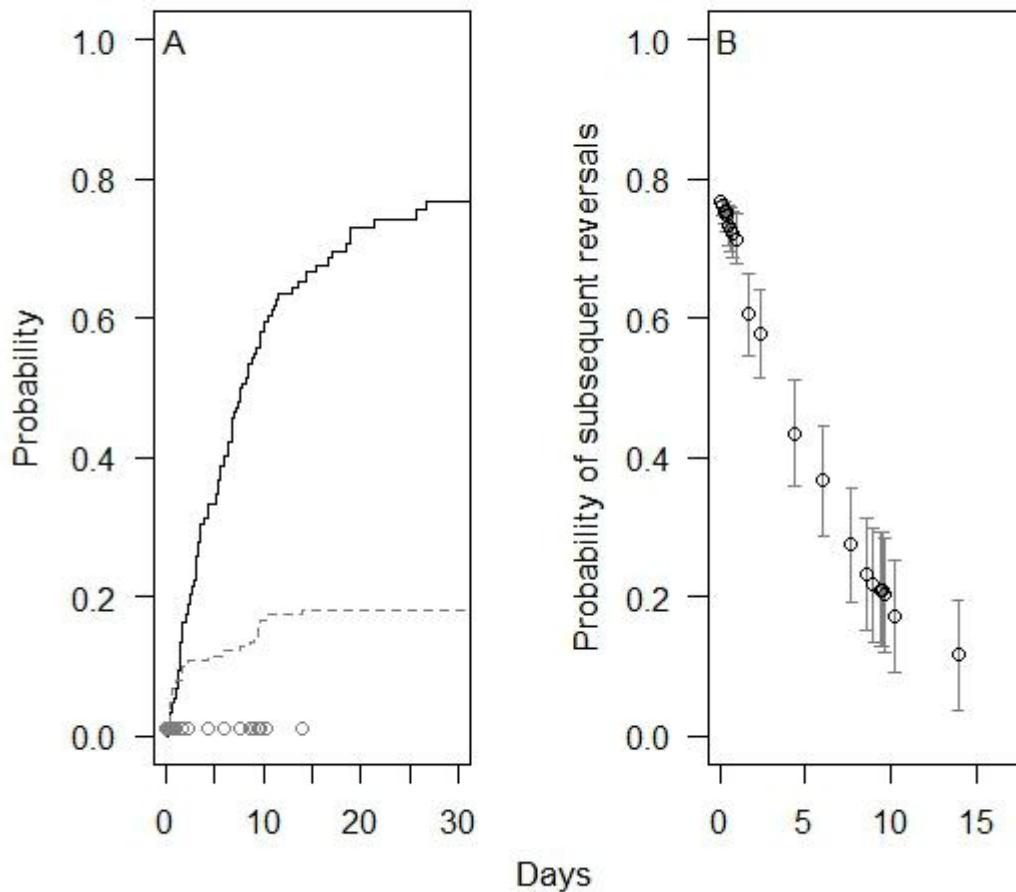


Figure 4.4 - (A) Cumulative incidence (cumulative probability) curves of likelihood of performing a migration reversal (solid black line) and likelihood of mortality without reversals (dashed grey line) as predicted by time (days) after saltwater entry. Grey circles at bottom of plot represent individual data points of time to mortality without reversals. (B) Estimated likelihood (open circle) and 95% confidence intervals (grey bars) that smolt which died would have exhibited reversals if they had survived, based on resampling with 5000 simulations.

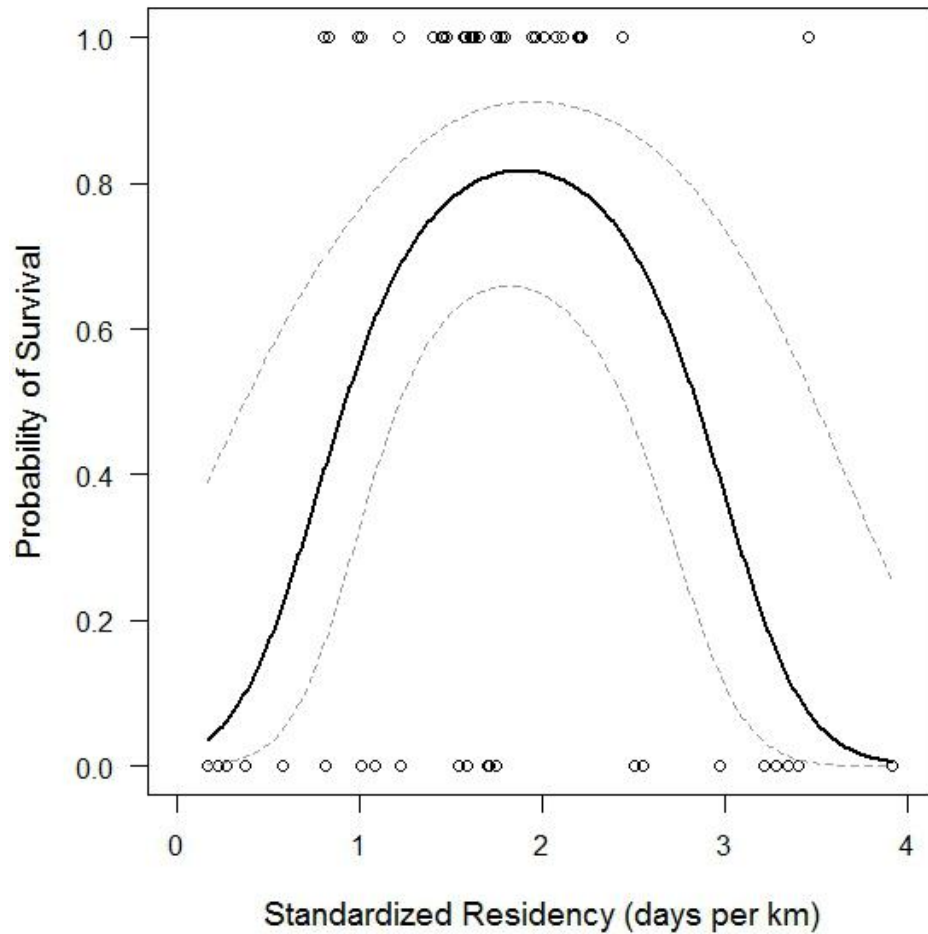


Figure 4.5 - The relationship between standardized ($\text{days} \cdot \text{km}^{-1}$) overall residency (SOR) and survival for smolts from the Gold River and West River 2010. Individual data points represent the binary fate of individual smolts (0 = died, 1 = survived) and the corresponding residency from release until death or exit of study area. Solid black line is the predicted logistic regression and dashed grey lines are the 95% confidence bands.

**CHAPTER 5: EFFECTS OF PREDATION ON TELEMETRY-BASED
SURVIVAL ESTIMATES: INSIGHTS FROM A STUDY ON ENDANGERED
ATLANTIC SALMON SMOLTS**

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5.1. ABSTRACT

Acoustic telemetry is increasingly being used to estimate population-level survival rates of fishes. However, these estimates may be impacted by detection efficiency of receivers and are reliant on the assumption that telemetry data represent the movements of the tagged (i.e. targeted) fish. Predation on tagged fish confounds survival estimates and, unlike the issue of detection efficiency, methods to deal with predation have yet to be developed. In an effort to incorporate predation into survival estimates, a suite of eleven summary migration metrics were compared between Atlantic salmon smolts (*Salmo salar*) and striped bass (*Morone saxatilis*) in 2008 and 2011. Cluster analyses revealed that 7% to 27% of tags implanted in smolts exhibited migration patterns similar to striped bass, which could be interpreted as evidence of predation. The “fate” of smolt tags detected exiting the study site was re-assigned as “predated / died” and subsequently, estimates of survival were adjusted accordingly. Compared to a traditional mark-recapture model, the cluster analysis-adjusted approach reduced estimated survival from 51.8% to 43.6% and from 36.4% to 24.3%.

5.2. INTRODUCTION

Quantifying the rate and timing of mortality is important for conservation planning for many fish populations, however, estimating these rates can be difficult given our inability to directly observe fish throughout much of their lives. Methods for estimating mortality rates have been developed based on traditional tagging and catch data (e.g. Seber and Le Cren 1967; Pollock et al. 1991; Pine et al. 2003), however recent advances in telemetry technologies that permit remote sensing of animal movement and behaviour are now providing new methods to estimate age- and stage-specific mortality rates, particularly at small temporal scales. One such technological advance has been acoustic telemetry which has facilitated the estimation of survival for freshwater and marine fish populations (e.g. Heupel and Simpfendorfer 2002; Melnychuk et al. 2007; Halfyard et al. 2013; Stokesbury et al. 2011). Survival estimates using acoustic telemetry

data are dependent on several critical assumptions, two of which are: (a) tagged fish are detected when in proximity to a receiver, and (b) detections of tags represent the movements of the fish into which the tags were implanted. The issue of tag detection probability has justifiably received increasing attention and analytical techniques such as mark-recapture modelling permit evaluation of the detection probability and also account for detection probability when estimating survival (e.g. Kocik et al. 2009; Davidsen et al. 2009; Halfyard et al. 2013). Conversely, the assumption that tag detection represents the movements of tagged fish has received very little attention and methods to identify predation/scavenging events using acoustic telemetry equipment are not well developed. A likely scenario that may violate this assumption is that tagged fish are consumed by a predator or scavenger, and the subsequent movement of the predator/scavenger is monitored while the active tag continues to transmit signals from within the gastrointestinal tract of the predator.

Based on assumed differences in the movements of prey and predators, apparent tag movements have been used to infer predation events. For example, apparent “reversal” migratory behaviour of Atlantic salmon *Salmo salar* L. 1758, smolts (i.e. alternating upstream and downstream movements) was interpreted by Beland et al. (2001) as potential predation by striped bass, *Morone saxatilis* (Walbaum, 1792). Likewise, the “disappearance” of tags from the study site prompted Halfyard et al. (2012) to conclude that salmon post-smolts were consumed by avian predators. Tag movement patterns have also been used to infer mortality in other species (e.g. Morrissey and Gruber 1993; Heupel and Simpfendorfer 2002; Karam et al. 2008). Ancillary sensor data, such as depth or temperature, can also provide evidence of predation events (e.g. Thorstad et al. 2011a), however, acoustic tags outfitted with sensors are larger than acoustic tags without sensors and may not be suitable for many small fishes. Ancillary sensor data from other telemetry technologies have been used to infer predation events (e.g. Béguet-Pon et al. 2012; Lacroix 2014; Wahlberg et al. *In Press*), but are similarly limited to large fishes. Therefore, there is a need for refined methods that can be used to identify potential predation events using small acoustic telemetry tags if acoustic telemetry is to be used to estimate mortality rates.

Atlantic salmon from the iBoF are currently listed as “Endangered” under the Canadian Species at Risk Act, and there is evidence that many populations are now extirpated (Gibson et al. 2004). Detailed information about the timing and magnitude of mortality is critical for the development of conservation and recovery plans for the endangered Atlantic salmon populations in eastern North America. In the case of inner Bay of Fundy (iBoF) Atlantic salmon populations, mortality during the estuarine and marine phase of currently limits population growth and has been responsible for the major declines that have placed these populations on the brink of extinction (Gibson et al. 2008). Sources of at-sea mortality remain unknown; however predation has been identified as a potentially important source of mortality (COSEWIC 2006; Lacroix 2014).

In this paper, we describe a study undertaken to estimate the estuarine survival of Atlantic salmon smolts from two iBoF salmon rivers. During the course of this study, it became apparent that many of the tag movements in one of the estuaries did not conform to expectations based on other smolt tracking studies, and that predation might be prevalent which would thus complicate direct interpretation of telemetry results. Striped bass are a predator that is abundant in the Minas Basin. There is public concern over the impact of predation by striped bass, and the potential effect of striped bass predation on Atlantic salmon conservation programs (Grout 2006). These concerns have been fueled, in part, by evidence of predation on smolts in salmon rivers in the Gulf of Maine (Blackwell and Jaunes 1998; Beland et al. 2001; Kocik et al. 2009), and also by divergent trends in the populations of salmon and striped bass. Fortuitously, a concurrent telemetry study for striped bass (Bradford et al. 2014) afforded the opportunity to compare the movements of tags placed in salmon smolts with tagged striped bass in one of the estuaries providing a potential mechanism to identify predation events. Here, we report survival estimates for these populations using three methods including a cluster analysis-based method that incorporates telemetry data on striped bass and multiple migration behaviour metrics. Although the cluster-based analyses likely do not fully account for predation effects, they do provide a basis to discuss the impact of failing to address predation when estimating survival from telemetry data. Implications of the study for recovery planning for iBoF salmon are also discussed.

5.3. METHODS

5.3.1. STUDY AREA AND POPULATIONS

The inner Bay of Fundy is a high-energy coastal area dominated by extreme tides. The iBoF can be subdivided into two basins, the Chignecto basin to the north and the Minas Basin to the south (Fig. 1). The Minas Basin is separated from the main basin of the Bay of Fundy by the Minas Passage; an approx. 5-6 km wide and 11km long restriction point through which as much as 15.3 km³ of water flushes with each tidal prism (i.e. the volume of water flushing between mean high and low tide), generating current speed in excess of 5 m·s⁻¹ (Amos and Long 1980). Tidal levels within the Minas Basin exceed 12 m (Thurston 1990) and at low tide expose extensive intertidal mud and sand flats.

Although Atlantic salmon likely used most accessible habitat at least intermittently in the past, there are 42 rivers and streams within the iBoF region thought to have supported salmon populations (DFO 2008). The abundance of adult salmon returning to iBoF rivers has been estimated to be about 40,000 salmon earlier in the 20th century (Amiro 2003), and abundance is thought to have declined to less than 250 adult salmon by 1999 (DFO 2008). Since the 1960's, abundance declines greater than 99% have occurred within individual populations (Gibson and Amiro 2003; Gibson et al. 2003), with a rapid rate of decline occurring since approximately 1990 (Gibson et al. 2008). Here, we report the results of a smolt tracking study for two of these populations: salmon in the Gaspereau and Stewiacke rivers. These populations differ in their ecology. Stewiacke River salmon mature predominantly as one sea-winter salmon with a comparatively higher frequency of repeat spawning (Chaput et al. 2006), and based on returns of Carlin tags from 1970 to 1990, appear to remain primarily within the Bay of Fundy and Gulf of Maine while in the marine environment (Amiro 2003). In contrast, a higher proportion of salmon in the Gaspereau River mature as two sea-winter salmon with a lower frequency of repeat spawning (Chaput et al. 2006), and based on tag returns from a similar time period, the marine migration of some portion of the population includes waters off West Greenland (Amiro 2003).

5.3.2. FIELD METHODS, TAGGING AND TELEMTRY

The movements and migration of Atlantic salmon smolts were monitored in the Stewiacke River (2008 and 2011) and the Gaspereau River (2011) using acoustic telemetry. In the Gaspereau River, smolts were captured in the White Rock bypass facility (a bypass at a hydroelectric installation located approx. 7.5 km above the head of the tide) while smolts on the Stewiacke River were captured using a rotary screw trap (E. G. Solutions, Corvallis, OR, USA) in 2008, or by angling with a single, barbless hook in 2011, 3.5 to 4.5 km above the head of the tide. In both rivers, these smolts were wild-acclimated fish, originally released as hatchery-origin fry 1-3 years prior.

Smolts were anaesthetized in 80-100 ppm of tricane methane sulphonate (MS222, Syndell Laboratories, Vancouver, BC, Canada), until reaching stage four anaesthesia, which, although partially dependent on water temperature, was generally in the range of 180 to 240 seconds. Smolts were then placed ventral-side up in a v-shaped surgery tray, and a soft rubber tube irrigated the gills of the fish with well-aerated water and a maintenance dose (30 ppm) of anaesthetic. Individually-coded acoustic tags (v9-6L, 3.6g in air, 9mm by 24mm, Amirix/Vemco, Halifax, N.S., Can.) were implanted in the intraperitoneal cavity via a single incision (approx. 12 to 15 mm in length) located immediately adjacent to the *linea alba* and immediately anterior to the pelvic girdle. Incisions were closed with three simple interrupted sutures using 4/0 absorbable monofilament. Post-surgery smolts were allowed to recover from the effects of anesthesia (approx. 24 hour), while in a streamside bin, prior to release. A total of 113 smolts, ranging from 120 to 210 mm fork length (L_F), were tagged between mid-May and early June (Table 1). The ratio of transmitter weight (2.9 g in air) to smolt weight in air averaged 7.5% (SD = 3.3%, max. 17.8%). Some salmon released in the Gaspereau River were implanted with larger pressure-sensing tags (Vemco V9P-2L). During surgery, it became apparent that these larger tags were impeding the swimming motion of these fish, and would therefore also likely impact migration behaviour and survival. This group of tagged fish was excluded from all analyses.

Acoustic receivers (Vemco VR2 and VR2W) were moored at various locations in the river and estuarine portions of each river (Fig. 1). Receivers were bottom-moored and fastened to a 0.5 m steel pole rising from an anchor, which was outfitted with a weighted drag line to aid in recovery. Additionally, as part of a fish tracking study to examine the potential for fish interactions with a tidal energy development site in Minas Passage (Redden et al. 2014), 38 receivers were deployed in the Minas Basin and Minas Passage in 2011 including a double “gate” of receivers ($n = 26$), spaced at 400 m intervals, traversing the east and west ends of the Minas Passage (Fig. 1). These receiver arrays, as well as the Ocean Tracking Network (OTN) line of 72 receivers spaced every 800 m seaward on the continental shelf near Halifax, NS (Ocean Tracking Network; Hebert et al. 2011) provided ancillary detections in the Minas Basin and the North Atlantic Ocean.

The tagging procedure can induce additional handling stress on smolts that may lead to tagging-induced mortality (e.g. Lacroix et al. 2004; Brown et al. 2010; Sandstrom et al. 2013). This may be an important consideration when estimating mortality rates. One method for dealing with tagging-induced mortality is to monitor the initial post-release movements of salmon smolts in an effort to determine if smolts died near the release site and assuming that these fish died as a result of the tagging procedure (e.g. Lacroix 2008; Halfyard et al. 2012). Thus, in addition to holding salmon for 24 hours after tagging prior to release, to account for tagging-induced mortality in this study, we estimated survival using only those smolts that reached the first downstream receiver. In the Gaspereau River, smolts not detected by one of the two most upstream receivers (max. 1.4 km from release site) were excluded from survival analyses ($n=5$). In the Stewiacke River, the first downstream receiver in both years either failed or failed to be recovered, leaving the next downstream receiver located 12.9 km (2008) and 5.5 km (2011) from the release site. In total, 25 (2008) and 5 (2011) salmon smolts failed to be detected by these receivers after release.

5.3.4. ANALYTICAL METHODS

All acoustic telemetry data were compiled in Vemco VUE software and subsequent analyses were conducted in R 2.6.0 (R Development Core Team; www.r-project.org). Initial analyses of the telemetry data led to the identification of several tags which exhibited behaviours that we considered atypical for Atlantic salmon smolts based on current knowledge of salmon behaviour in estuaries. For example, one salmon tag was detected exhibiting migration reversals within the Stewiacke and Stewiacke estuaries before reaching the mouth, and was subsequently detected travelling along the southern shore of the Minas Basin. This tag was detected entering the Gaspereau River estuary (approx. 38 hours after exit of Shubenacadie estuary) and ascending the Gaspereau River to a point immediately downstream from the head of tide (HoT) where it was continuously detected for 18.3 days prior to its final detection (despite several receivers located both downstream and upstream). Striped bass are known to enter the Gaspereau River at this time of year and the area supports a popular recreational fishery. Additionally, several Stewiacke River salmon smolts ($n = 7$) were detected in the Shubenacadie River, 3.8 km upstream above the confluence of the Stewiacke and Shubenacadie River (receiver SH.8). Others appeared to make repeated migration reversals in an area known to be the spawning habitat of striped bass. While it cannot be confirmed what these behaviours actually represent, one potential explanation is that these tags had been consumed by striped bass, which are common in the Minas Basin and are particularly abundant in the Stewiacke and Shubenacadie Rivers when spawning in May and June (Bradford et al. 2012).

The identification of potential predation events led us to question the utility of estimating survival using conventional analyses. Providing the most accurate estimates of smolt survival requires considering all potentially confounding effects, most notably the effect of gear performance (i.e. detection probability) and the confounding effects of predation. To this end, we calculate and compare four methods to estimate survival, including (1) a basic ratio-based method, (2) a mark-recapture model approach that accounts for detection probability, (3) a novel cluster analysis of behavioural characteristics used in an attempt to identify tags within the gut of a predator, and (4) a

combined cluster analysis-based adjusted mark-recapture method that accounts for both predation and gear performance.

5.3.5. *ANALYTICAL METHODS: RATIO-BASED SURVIVAL ESTIMATES*

Survival estimates were first calculated without correcting for predation effects and assuming 100% detection efficiency. These ratio-based estimates of survival were derived by dividing the number of salmon smolts detected at the mouth of the estuary (i.e. SH.11 or G.5 in Fig. 1) by the number of salmon smolts detected at the first receiver downstream from the release site (to account for potential tagging related mortality).

5.3.6. *ANALYTICAL METHODS: CJS SURVIVAL ESTIMATES*

In order to account for receiver detection efficiencies less than 100% and differences in detection efficiency among receivers, we estimated survival using Cormack-Jolly-Seber (CJS) mark-recapture models (Cormack 1964; Jolly 1965; Seber 1965); a technique that has previously been applied to Atlantic salmon telemetry data (e.g. Lacroix 2008; Kocik et al. 2009; Halfyard et al. 2013). Because the migration of salmon smolts is ultimately unidirectional (i.e. they move from the river to the ocean), and this migration corridor is bounded by land on two sides, the statistical sampling “events” are each receiver location, and the distance between each receiver is considered the sampling interval across which survival was estimated (Halfyard et al. 2013). Survival rates were standardized by the distance between receivers ($S \cdot km^{-1}$). All models used the logit link function.

A fully-parameterized global model was compiled for each of the three river-year combinations, where survival and detection probability was calculated for each receiver interval (i.e. dependent on distance from HoT), with release group effects, and the interactions of these parameters. In an effort to assess whether the global model adequately fits the data, a goodness-of-fit parameter (\hat{c}) was estimated using the bootstrap method with 200 simulations (Burnham and Anderson 2002). Comparing the fit of a

model with reduced parameters to the global model is only informative if the global model adequately fits the data (Burnham and Anderson 2002).

From each of the three global models, a pool of nested models was derived and Akaike information criterion (AIC) values were calculated for each of these models. AIC addresses issues of balance between under- and over-fit models and formally weighs model bias and variance trade-offs (Burnham and Anderson 2004). In cases where \hat{c} was > 1.0 , these models were adjusted for lack-of-fit (i.e. over-dispersion), and thus a quasi-likelihood AIC values (QAIC) were calculated. Because the number of parameters being estimated was often high relative to the data sample size, a bias adjustment was made that resulted in the calculation of a second order AIC value (AICc) or QAIC value (QAICc). In all cases, several models showed utility in describing the data. Thus in an effort to incorporate the uncertainty of all suitable models, final parameter estimates were derived via weighted (by AIC values) model averaging (Johnson and Omland 2004).

5.3.7. ANALYTICAL METHODS: CLUSTER ANALYSIS-BASED SURVIVAL ESTIMATES

While attempting to address the confounding effects of predation, a concurrent telemetry study on striped bass provided an opportunity to compare the movements of the two species in the Stewiacke River estuary. This striped bass project used data that were collected in the same area and using the same acoustic receivers. Striped bass were captured in a trap net and tagged with acoustic tags (Vemco V13TP-2L) in the upper Shubenacadie River (Bradford et al. 2014) as they exited their over-wintering habitat in a large headwater lake *en route* to their spawning grounds in the Stewiacke River estuary. Data from 31 striped bass were included from the 2008 season with a mean total length of 712 mm (sd=109 mm, range=(410 mm, 898 mm)) and data from 13 striped bass were included from the 2011 season with a mean total length of 654 mm (sd=66 mm, range=(545 mm, 780 mm)).

Cluster analyses were used to highlight structuring among tags of the two species, where smolt tags that behaved more similar to striped bass than other salmon smolts may represent predation events. Cluster analysis involved three primary steps; 1) selection of

variables to include in the analysis, 2) selection of an appropriate dissimilarity matrix, and 3) selection of an appropriate method of clustering.

We selected eleven (ten in 2011) summary variables that described the movement patterns of acoustic tags to create a multivariate data matrix. These variables were largely selected on the basis of prior assumptions of how the migratory behaviour of salmon smolts and striped bass may differ in this area. Variables included those related to detection patterns (*a.* total number of detections, *b.* total days with detections, and *c.* total time between the first and last detection) and also those related to estimated movement parameters for each tag (*d.* total tag displacement (i.e. distance travelled), *e.* mean upstream velocity, *f.* maximum upstream velocity, *g.* mean downstream velocity, *h.* maximum downstream velocity, *i.* the total number of migration direction reversals, *j.* the total time spent on the purported spawning grounds for striped bass), and *k.* total detections in the Shubenacadie River above the confluence with Stewiacke River (SH.8, Fig. 1, available only in 2008). Values for each variable were calculated for each tag in each species constrained to the time period when smolt are present in these estuaries; May 23rd to June 23rd (2008), and May 25th to July 6th (2011). Striped bass data were similarly confined to these time periods.

Empty matrix cells were assigned a zero, as missing cells were ‘non-ignorable’ (Quinn and Keough 2002) and represented actual differences in fish behaviour and not gear malfunctions (e.g. no upstream migration speed estimate due to downstream-only migration). Date used in the matrix were scaled and because we wanted to compare between individual tags using quantitative data (i.e. a Q-mode association measure), we constructed a symmetrical distance matrix using “Euclidean” distance (Legendre and Legendre 1998; Borcard et al. 2011).

A hierarchical clustering approach using Wards minimum variance method was selected and the analysis was implemented using the ‘hclust’ function in the ‘base’ package of R 2.6.0 (R Development Core Team; www.r-project.org). This analysis begins by determining the two tags with the shortest Euclidean distance between them, and pairing these two tags together as a single cluster. Wards method then uses a centroid

link to identify the mean distance of this new cluster, and then compares it to all other distances. The process of clustering based on minimum distance is repeated until the desired number of clusters is achieved. To determine the appropriate number of clusters to accept, we used the broken stick model (Bennett 1996) which plots the cumulative variance explained by the number of potential clusters. The point at which there is a sharp decline in the slope of the cumulative curve is used to determine the appropriate number of clusters. Estimating the point at which a “sharp decline” occurs is partially subjective, however the between-tag structuring of the resultant cluster dendrogram would remain the same regardless of number of clusters.

To test the magnitude by which certain migration parameters influenced the outcome of the cluster analyses, we conducted an incomplete sensitivity analysis where varying combinations of input parameters were excluded from the analyses. In addition to the full model that included all parameters, between six (2008) and four (2011) subsets of parameters were tested. Input parameters for each of the four trials were as follows; trial 1 (all parameters less the total time on spawning grounds), trial 2 (all parameters less the total number of reversals and total displacement), trial 3 (all parameters less the four speed metrics), and trial 4 (all parameters less the total number of detections and the total number of days with detections). Using the 2008 data, trial 5 consisted of all parameters less the total detections in the Shubenacadie River above the confluence with Stewiacke River (receiver SH.8). Trial 6 consisted of only the total number of reversals, the total time on spawning grounds, and the total detections in the Shubenacadie River above the confluence with Stewiacke River.

Cluster analyses identified similarities in the migration movement patterns among tags. We assumed that predation had occurred when smolt tags clustered among striped bass tags, however interpreting these clusters was partially subjective and warranted (particularly in 2011) post-hoc examination of differences in the average migration metrics for each cluster. Cluster analyses identified individual smolt tags that were detected exiting the river but could be re-assigned as having died (i.e. predation), providing the opportunity to directly adjust ratio-based survival estimates.

5.3.8. ANALYTICAL METHODS: COMBINED CLUSTER ANALYSIS AND CJS SURVIVAL ESTIMATES

Finally, by merging the cluster results with the CJS survival estimates, we were able to estimate survival after accounting for both detection efficiency and predation. We constructed contingency tables for both years where we had cluster analyses using the variables; detection at the mouth of the estuary based on CJS model results and re-assignment of presumed fate based on cluster analyses. Thus, the contingency table was populated based on the proportions of smolt tags that were classified into one of four categories: smolt tags detected at the mouth of the estuary and either re-assigned as within striped bass (P_{DR}) or remained assigned as survivors (P_{DS}) and smolt tags that were undetected at the mouth and either re-assigned as within striped bass (P_{UR}) or remained assigned as survivors (P_{US}). The proportion of tags that were detected, (P_D) is equal to the ratio-based estimate of survival and the cluster analyses permitted estimation of P_{DR} and P_{DS} . The proportion of tags that were not detected (P_U) is the difference between the CJS and ratio-based survival estimates. To estimate P_{UR} and P_{US} independently we assumed that the risk of predation was similar for both detected and undetected tags and applied the proportion of re-assigned tags for those that were detected (i.e. P_{DR} and P_{DS}) to the estimate of P_U . The final cluster analysis-adjusted CJS survival estimate (P_S) was calculated as the sum of the proportions of detected tags and undetected tags that were survivors ($P_{DS} + P_{US}$).

Finally, detections on receivers within the Minas Basin, the Minas Passage and on the Halifax line of receivers were used to help derive estimates of survival to mouth of estuaries (i.e. used as subsequent encounters in the CJS model). Additionally, in the context of recovery planning, detections on these receivers are also informative about minimum survival to these locations, after considering the significant caveats of unknown detection efficiency and marine migration routes.

5.4. RESULTS

5.4.1. RATIO-BASED SURVIVAL ESTIMATES

A total of 78 salmon smolts were detected on the first receiver downstream from their respective release sites, Salmon not detected downriver of their release site ($n = 35$) represent the sum of losses related to handling/tagging effects, and predation and other sources of natural mortality. In general, the proportion of tags detected decreased with distance from release (Table 2). In the Stewiacke River, the absolute number of detections was highest in the area immediately downstream from the head-of-tide while the distribution of absolute detections in the Gaspereau River was fairly homogenous.

For the Stewiacke River, 19 smolts were detected at the mouth of the Shubenacadie River estuary (i.e. entering the Minas Basin) in 2008 and six smolts were detected in 2011, resulting in a ratio-based estimate of 46.3% and 27.3% survival from the most upstream receiver location (1.7 km downstream from HoT), respectively. In 2008, the proportion of detected tags at the mouth of the estuary was much higher for the two release events in May than for the two release events in June. For the Gaspereau River in 2011, eight unique tags were detected at the mouth of the estuary, resulting in a ratio-based survival estimate of 53.3% from the most upstream receiver location (6.2 km upstream from HoT). The deployment of receivers in the Minas Basin and Minas Passage in 2011 permitted additional detections which partially accounts for surviving salmon that reached the Minas Basin but were not detected at the river's mouth. These detections increased the estimated survival from 27.3% to 36.4% for the Stewiacke River in 2011 (i.e. two additional salmon), however the Gaspereau River estimate was unchanged. Detections in the Minas Basin were widespread and occurred at the following locations (some on multiple receivers); Gaspereau River: Avon ($n = 3$), Walton ($n = 4$), Five Islands ($n = 1$), and Minas Passage ($n = 7$); Stewiacke River: Walton ($n = 3$), Five Islands ($n = 1$), Kingsport ($n = 1$), and Minas Passage ($n = 2$).

The efficiency of the receivers in the Minas Passage is known to be highly variable (Redden et al. 2014), however if we consider detections in the Minas Passage as a minimum estimate of survival to the Minas Passage, then minimum survival in the

Minas Basin is estimated as 25.0% and 87.5% for the Stewiacke and Gaspereau Rivers, respectively. This would lead to a cumulative ratio-based estimate of minimum survival from the head of tide to the Minas Passage of 9.0% (Stewiacke R.) and 46.7% (Gaspereau R.).

5.4.2. CJS-BASED SURVIVAL ESTIMATES

To account for the bias in survival estimates that occurs if not all fish passing by a receiver are detected, survival was also estimated using CJS models. Goodness-of-fit testing of the global model in each dataset suggested that all models adequately fit the data, although there was some evidence of significant, albeit mild, lack-of-fit in all datasets ($\hat{c} = 1.99$, $\hat{c} = 1.25$, $\hat{c} = 1.13$ in the Stewiacke River 2008, 2011 and Gaspereau River 2011, respectively).

Using the Stewiacke River 2008 data, it was clear that only a single model was supported (QAICc weight > 0.99), and this most parsimonious model suggested that both survival and detection probabilities were a function of distance from HoT and survival was independent of release group (Table S-1). Model averaged survival estimates (also weighted almost exclusively by the most parsimonious model) ranged from $0.953 \cdot \text{km}^{-1}$ to $1.000 \cdot \text{km}^{-1}$, exhibited minima within the Stewiacke River estuary (Fig. 2), and resulted in an overall cumulative survival to the mouth of the Shubenacadie estuary of 0.554.

In the Stewiacke River 2011, although there was support for several models, the QAICc weight for most parsimonious model was approximately six-times larger than the next best model (Table S-1). The most parsimonious model suggested that survival was a function of distance from release while detection probability was constant at all receivers. Model-averaged survival estimates ranged from $0.809 \cdot \text{km}^{-1}$ to $0.996 \cdot \text{km}^{-1}$, exhibited a minimum survival within the Stewiacke River estuary (Fig. 2), and resulted in an overall cumulative survival to the mouth of the Shubenacadie estuary of 0.364.

Finally, there was also support for several models using the Gaspereau River 2011 data; however the QAICc weight for most parsimonious model was approximately eight-times larger than the next best model (Table S-1). The most parsimonious model suggested that survival was a function of distance from release while detection probability was a constant function. Model- averaged survival estimates ranged from $0.940 \cdot \text{km}^{-1}$ to $0.997 \cdot \text{km}^{-1}$, exhibited a minimum survival near the seaward extent of the Gaspereau River estuary (Fig. 2), and resulted in an overall cumulative survival to the mouth of the Gaspereau estuary of 0.540. All models account for tagging-induced mortalities and estimated survival in the first interval (i.e. receiver spacing) reflects this censoring by estimating 100% survival.

5.4.3. CLUSTER ANALYSIS-ADJUSTED RATIO-BASED SURVIVAL ESTIMATES

Cluster analysis revealed substantial structuring in the movement of the tags in both years, however, there was greater differentiation between the movements of fish in the Stewiacke River in 2008 than in 2011. In 2008, there was evidence of three major clusters; one containing predominantly salmon smolts (except a single striped bass, cluster 1, Fig. 3), one containing exclusively striped bass (cluster 3, Fig. 3) and one containing predominantly striped bass with three salmon smolts (cluster 2, Fig. 3). A qualitative generalized assessment of migration tracks indicated that tags clustered in the predominately salmon smolt group showed short and unidirectional movements while tags in the other two clusters exhibited more extensive tracks with frequent migration reversals, particularly near the striped bass spawning grounds (Fig. 4). Comparison of the movement and detection metrics between the clusters indicated that, relative to the other two clusters, the cluster of predominately salmon smolts (cluster 1) was characterized by fewer total detections, days with detections, number of migration reversals; and lower total displacement, total time lapse, time on the striped bass spawning grounds, and migration (Table 3). Only 4 of 37 salmon tags in this group were detected in Shubenacadie River (receiver SH.8) above its confluence with the Stewiacke

The sensitivity analyses indicated that the clustering of Stewiacke 2008 data (not shown) was robust with regard to the selection of input parameters. A total of three unique salmon tags clustered with striped bass in the full model, a result that did not change when the cluster analyses were done with subsets of parameters. All three of the salmon tags that clustered with the striped bass were initially classified as having exited the river (i.e. survived) as all were detected at the mouth of the Shubenacadie River.

In the Stewiacke River in 2011, interpretation of the cluster analysis was less clear: while there was evidence of structuring, the clusters were more similar than in the 2008 data (Fig. 5). The full model indicated relatively high separation of two clusters of tags from the remaining tags and each other. Subsequent sensitivity analysis confirmed that these two clusters were common among all permutations of input parameters that were tested with the exception of the trial which excluded the four speed-related parameters (Table 4). First, one salmon tag and either one or two striped bass tags constantly grouped as outliers (cluster 1). These tags exhibited extreme values of all parameters, most typified by numerous reversals, extended time spent on the spawning grounds and a well-populated detection history with many detections (Table 5). Second, a cluster of seven salmon tags (cluster 2) showed substantial segregation from the remaining tags in the full model and four of five models run with subsets of data (not evident in subset excluding speed data). These salmon exhibited generally unidirectional movements downstream as far as the spawning grounds (or 1 short term and small scale reversal), after which their tags were lost. All migration metrics for these salmon were consistently the lowest of all tags

There was structuring within the remaining tags; however interpreting this structure was partially subjective and dependent on the input parameters. Nonetheless, the results from full model and three of four sensitivity trials suggest that there may be two additional clusters within the remaining tags that display distinct migration patterns. Both clusters included a mixture of salmon smolts and striped bass. If we compare these final two clusters from the full model results, tags in cluster 3 generally exhibited prolonged residency on the spawning grounds with more frequent migration reversals and longer detection histories (although shorter than those “outlier” tags identified in cluster 1).

Conversely, cluster 4 was typified by tags that exhibited relatively few reversals, minimal time on the spawning ground and relative short detection histories (Table 5).

If the salmon tags that cluster with striped bass reflect predation events (i.e. smolt tags are detected while in the gastrointestinal tract of striped bass), then accounting for this predation would improve the survival estimates. More specifically, those tags detected exiting the river and originally assumed to represent surviving salmon could be reclassified as predation-related mortalities. This reclassification reduces the ratio-based survival rate estimates for Stewiacke River smolts from 46.3 to 39.0% in 2008 and from 36.4 to 27.3% in 2011. Further, if we assume that the proportion of smolts that cluster with striped bass represent the true portion of smolts consumed by striped bass (*see* Discussion), then minimum overall estimated predation rates based on the cluster analyses are 7.3% and 27.3%, in 2008 and 2011 respectively.

5.4.4. COMBINED CLUSTER ANALYSIS-BASED AND CJS SURVIVAL ESTIMATES

In order to derive survival estimates that account for both detection efficiency and the confounding effects of predation, we integrated the results of the full cluster model, the CJS models (cumulative estimates), and the ratio-based estimates of survival in contingency tables for the Stewiacke River in 2008 (Table 6) and in 2011 (Table 7). As expected, the estimates provided by combining the model results were lower than CJS-only estimates as a portion of the undetected fish estimated by the CJS model were re-assigned as within striped bass. Compared to the CJS model results, the cluster analysis-adjusted approach reduced estimated survival from 51.8% to 43.6% and from 36.4% to 24.3%.

5.4.5. EXTENSION OF CLUSTER ANALYSES TO DESCRIBE BEHAVIOUR

Identifying salmon behaviour is similarly difficult given the confounding effects of predation on migratory behavior. However, if we remove tags classified as having been preyed upon using the cluster analyses, variables such as residency times in

estuaries can be better estimated. For example, in the Stewiacke River 2011, analysis of all data suggest that salmon reached the mouth of the estuary after 9.8 ± 6.8 days ($n = 6$, mean \pm SD), however after removing those tags suspected to be in striped bass, residency estimates are reduced to 5.5 ± 1.2 days ($n = 4$, mean \pm SD). Likewise, estimates of residency to the mouth of the estuary in the Stewiacke River in 2008 were reduced from 6.2 ± 5.5 days ($n = 16$, mean \pm SD) when using all tags, to 5.3 ± 4.3 days ($n = 15$, mean \pm SD) after removing a single tags suspected to be in a striped bass. It was not possible to perform similar adjusted estimates of residency in the Gaspereau River (because no cluster analysis was feasible), however using the entire data set, postsmolts reached the mouth of the estuary after only 3.0 ± 1.2 days (mean \pm SD).

5.4.6. MIGRATION THROUGH THE MINAS PASSAGE AND TO THE HALIFAX LINE

Salmon also appear to exit the Minas Basin rapidly. Gaspereau River ($n = 7$) and Stewiacke River ($n = 2$) smolt tags were detected in the Minas Passage between May 23rd and June 12th 2011, equating to an average of 8.2 days post-release (SD = 2.2) or an average 5.0 days after exiting their respective estuaries (SD = 2.1). None of the three Stewiacke 2011 tags that were re-assigned as within striped bass via cluster analysis were detected at the Minas Passage. Of the salmon detected traversing the Minas Passage, three postsmolts from the Gaspereau River were also subsequently detected on an array of receivers located near Halifax, N.S. Postsmolt detections on the Halifax line of receivers occurred between June 12th and June 19th 2011, which is between 16.9 to 25.6 days after detection on the Minas Passage line. Assuming postsmolts migrated along the shortest route, these detections would infer minimum migration rates between 21.5-32.6 km \cdot d⁻¹ (or between 1.35 and 1.88 body-lengths \cdot s⁻¹, based on body length at time of capture).

5.6. DISCUSSION

5.6.1. *EFFECTS OF PREDATION ON SURVIVAL ESTIMATES*

Virtually all telemetry studies rely on the assumption that detection of the tag represents a detection of the individual animal to which the tag was affixed. Here, we add to the evidence that, in some cases, this assumption may be incorrect and failing to consider the potentially confounding effects of predation can lead to misinterpretation of telemetry data and, ultimately, inaccurate estimates of fish movement, behaviour and survival. Evidence of striped bass predation was provided by our findings of unexpected movements of salmon tags and, more importantly, the similarities of movement metrics between predatory striped bass and some salmon tags. Unexpected tag movements have been previously interpreted as evidence of predation (e.g. Beland et al. 2001; Vogel 2010; Thorstad et al. 2011a), although this study is among the first to account for the confounding effects of predatory fishes through comparison of movement metrics (but see Romine et al. 2014).

The purpose of applying of cluster analyses to summarized movement and detection parameters was to identify movement patterns of the two species. We assumed that salmon smolts could exhibit one or more unknown migration patterns (e.g. Hedger et al. 2008; Halfyard et al. 2012), but that detections of striped bass tags represented the movements of striped bass (i.e. they were not at risk to natural predation) and thus we could identify all patterns in the movement of striped bass. We also assumed that these two species would exhibit dissimilar migratory behaviour given the significant differences in body size (smolt length ca. <0.2m vs. striped bass length ca. 0.4-0.9m) and purpose of migration. Atlantic salmon smolts are generally thought to transit estuaries rapidly enroute to marine habitats (Hansen and Quinn 1998; Thorstad et al. 2011b), while striped bass in this area are primarily spawning (Douglas et al. 2003), but also apparently foraging. Therefore, our assumption that migration patterns which are similar between salmon smolt tags and striped bass represented a predation event may be reasonable. The identification of common movement patterns was well supported by cluster analyses however interpretation of each cluster was partially subjective. Clustering results in 2008

were relatively easy to interpret as only two behaviours were identified, one exhibited primarily by salmon smolts and the second exhibited primarily by striped bass. Thus, smolts that ‘behaved’ like striped bass could be reasonably assumed to have been consumed. A single striped bass grouped with salmon smolts in 2008. We interpreted this phenomenon as a result of restricting the data from striped bass to the period when smolt were present. For these striped bass tags, additional detections prior to the smolt ‘window’ showed more extensive movements but these detections were not reflected in the cluster analyses.

The 2011 data were considerably more difficult to interpret, largely due to the increased variability in striped bass behaviour. Only one cluster contained exclusively salmon smolts while all other contained a mixture of species. We interpreted salmon in two of these clusters (1 and 2) as evidence of predation while interpreted the remaining cluster as salmon plus striped bass with less extensive detection histories compared to other striped bass. An alternative interpretation of this cluster is that these salmon also represent predation event which would further reduce overall smolt survival (to near zero) and increase the estimated predation rate.

However, cluster analysis does assume that adequate migration parameters have been analyzed to identify all migration patterns and, subsequently, predation events. Although the results of our sensitivity analyses provide some confidence that results would not change by using subsets of the migration parameters we outline, it is possible that additional migration parameters not considered in this study may provide more information on migration.

Migration parameters represented the mean values across the entire migration for each individual. As a result, we assume that smolts were consumed early enough to affect the mean of these migration parameters. If predation occurs late, the overall metrics for smolt tags would reflect primarily valid smolt movements. Because migration parameters are the means across the migration period, we are unable to identify the timing of predation (i.e. when detections switch from representing smolts to striped bass). For this reason, encounter histories denoting the movements of individual tags (used in CJS mark-

recapture models) cannot be ‘adjusted’ to reflect the timing of predation (i.e. discounting detections after the presumed timing of predation), therefore the results of cluster analyses can only be used to offset cumulative CJS survival estimates or ratio-based estimates.

Additionally, the retention time of acoustic transmitters within the gastrointestinal tracts of striped bass is unknown and variable rates of tag retention may impact the ability to detection predation events. Data from other predatory species may highlight the potential expected range for intragastric tag retention. For example, Atlantic cod *Gadus morhua* that voluntarily ingested transmitters retained these tags between 44 and 77 days (Winger and Walsh 2001), although earlier work reported evacuation in as little as 5 days (Armstrong et al. 1992). Similarly, voluntary ingested acoustic tags by several shark species were retained for as little as 1 day, but averaged 6.8 days (Brunnschweiler 2009), although the presence of a fishing hook attached to some of the tags likely affected these results. In general, gastric evacuation rates of fish are highly variable and dependent on factors including; predator size, meal size, and water/body temperature (Jobling et al. 1977; Durbin and Durbin 1980; Rogers and Burley 1991). .

Advancing cluster analysis-based techniques for identifying predation using telemetry data should determine clear *a priori* expectations of the potential diversity of movement patterns and tailor receiver deployment as such. In particular, designing studies to provide sufficient detection histories to permit chronological clustering (e.g. Legendre et al 1985) may identify the timing of predation and permit integration with mark-recapture models. State-space modelling of telemetry tags (Jonsen et al. 2003) in linear systems such as rivers and estuaries may also provide benefits such as the ability to identify hidden behaviour “states” that may refine the identification of predation. Technological advances in telemetry techniques should also be pursued to provide additional certainty when identifying predation. In particular, sufficiently reducing the size of sensor tags capable of identifying predation events (e.g. Béguer-Pon et al. 2012; Lacroix 2014; Wahlberg et al. *In Press*) so that they may be used in juvenile fishes such as salmon smolts will be important. Further, the development of new sensor tags capable

of specifically identifying predation events should be a priority and will permit more direct ‘observation’ of predation rather than inferring predation events.

5.6.2. IMPLICATION OF RESEARCH FOR THE RECOVERY OF iBoF SALMON

It has been hypothesized that many iBoF salmon populations exhibit localized residency within the Bay of Fundy (Jessop 1976; Ritter 1989; Amiro 2003; COSEWIC 2006) and telemetry of post-smolts from several Bay of Fundy rivers (including iBoF rivers) suggests that between 29% and 90% of surviving smolts remain within the Bay of Fundy throughout the summer (Lacroix et al. 2005, Lacroix 2008). Conversely, there is evidence that salmon from the Gaspereau River may be anomalous within the iBoF. Tagged salmon from the Gaspereau River have been captured in commercial fisheries in Newfoundland and also Greenland (COSEWIC 2006). Detections in the Minas Passage suggests that post-smolts exited the Minas Basin rapidly, however, the detection of three Gaspereau River smolts on the Halifax line of receivers between 17 and 26 days later suggest they continue their migration toward the purported feeding grounds of the Labrador sea and south Greenland (Reddin 1988, Ritter 1989). Differences between the two populations in the number of post-smolts detected at both the Minas Passage line and the Halifax line of receivers are consistent with the potentially different migration strategies used by these two populations.

The estimated survival rates reported in this study suggest that estuarine and early marine survival may vary between iBoF rivers and between years within a river. Differences in survival rates between the Gaspereau and Stewiacke Rivers in 2011 may reflect the predation intensity to which smolts are subjected. Although there would be abundant predators in both estuaries, the aggregation of spawning striped bass in the Stewiacke River provides a substantially higher concentration of potential predators than in the Gaspereau River.

Regardless of which method was used to calculate survival, the estimates provided here were lower than previously reported for these two study rivers, other iBoF rivers and other rivers within eastern Canada (Table 9). A potential explanation for

declining survival between 2002 (Lacroix 2008) and 2008-2011 (*this study*) may be related to an increasing abundance of predators within these estuaries and the iBoF. Striped bass are likely the most common predator within this area, and although a time series of population abundance is not available for the Shubenacadie – Stewiacke River striped bass population, there is some anecdotal evidence abundance has increased. For example, the province of Nova Scotia conducts a survey of recreational anglers every five years. There has been increases in catch-per-unit-effort (0.9 to 1.4), total catch (30 790 to 94 700) and the number of anglers pursuing striped bass (4217 to 7248) between 2000 and 2010 (NSDFA 2002, 2013), suggesting that the abundance of striped bass has increased¹.

Subject to the caveats associated the use of behavioural modelling to identify predation events, the minimum level of predation by striped bass estimated in this study for Stewiacke River smolt (7.3% in 2008 and 27.3% in 2011) is roughly 13 to 36% of the total mortality estimated to have occurred in the estuary (56.4% and 75.7% in 2008 and 2011 respectively). While we cannot preclude the possibility that predation events were not accurately identified via the behavioural modelling (i.e. salmon that failed to reach the mouth of the estuary were eaten by striped bass but did not cluster with striped bass), these results may indicate that other factors in addition to striped bass predation are effecting the survival of smolts in this estuary.

Irrespective of whether predation events by striped bass were accurately identified in the study, the results of this study are informative about the magnitude of mortality occurring in the estuary relative to the total mortality occurring between the smolt and returning adult life stages, and whether increases in survival in the estuary would be sufficient to prevent the extirpation of salmon in these rivers. Smolt-to-adult return rates from the Gaspereau River smolt cohort of 2002 (wild-reared) was estimated at 0.8% (Gibson et al. 2004). Return rates in the Stewiacke River are unknown; however it is

¹ This fishery occurred primarily within the Minas Basin, although smaller fisheries occurred along the Atlantic coast of Nova Scotia and elsewhere along the Nova Scotia side of the Bay of Fundy. Angling in tidal waters in Nova Scotia does not require a license and thus these trends represent only volunteer information on marine fisheries conducted by licenced freshwater anglers and may not adequately describe catch trends.

suspected that they are similar to those in the Gaspereau River or the Big Salmon River, NB, where the return rate for the 2002 wild-reared smolt cohort was estimated at 0.3% (Gibson et al. 2004). These rates are low relative to those from the past: return rates for salmon in the Big Salmon River averaged 4.67% for the 1966 to 1971 time period (Ritter 1989). If we assume a return rate of 0.5% for both populations at present, and use survival estimates generated in this study, it is apparent that mortality is very high later in the marine phase of their life cycle. For example, using the estimated survival rates to the Minas Passage of 46.7% (Gaspereau R. 2011) and 9.0% (Stewiacke R. 2011), values that could be considered minima because they are not corrected for detection efficiency (unknown at this location), then survival from the Minas Passage to the returning adult stage would not be more than 0.01% and 0.06% for the Gaspereau and Stewiacke populations, respectively. Additionally, three smolts from the Gaspereau River were detected on the Halifax line, leading to the inference that survival cannot be greater than 0.03% from this time until returning to the river to spawn.

For these reasons, conservation measures aimed at reducing salmon mortality within iBoF estuaries and the Minas Basin are not expected to produce significant population responses. For example, if estuarine mortality could be reduced by as much as 25% (i.e. before reaching the Minas Basin), marine return rates would increase from 0.5% to 0.6% (Gaspereau R. 2011 and Stewiacke R. 2008) and 0.7% (Stewiacke R. 2011). Even at these increased return rates, the probability of extirpation within three-generations for these populations would remain near one (Gibson et al. 2008).

5.6.3. CONCLUDING REMARKS

Although the results of analyses presented in this paper should not be considered definitive, there was sufficient evidence to suggest that: a) the confounding effects of predation on survival estimates derived from acoustic telemetry data is a potentially serious issue, b) further development of methods to identify predation on tagged animals is warranted, and c) the issue of predation by striped bass on iBoF salmon warrants consideration during conservation planning.

With respect to effects of predation on acoustic telemetry-based survival estimates, it is presently unclear whether predation events can be identified via analyses of behaviours, particularly in the absence of clear, *a priori* knowledge of the differences in migratory behaviour between or among species. Even when these differences are known, misclassification can still occur if predation events occur late during the migration; because the majority of the track would still resemble that of a smolt. As an alternative to analytical methods, development of tags that could identify predation events could lead to a more direct resolution of the confounding effects of predation on survival estimates.

The results of this study do highlight a potential conflict between a predator and endangered populations of Atlantic salmon. However, because the Shubenacadie-Stewiacke population of striped bass is part of a larger population assemblage also designated “endangered”, conservation measures aimed at reducing the abundance of striped bass are not likely to be palatable. A potentially useful implication of these findings is the tailoring of conservation measures to maximize survival during this early period. For example, the release of hatchery-origin smolts in the Stewiacke River could be timed to avoid the highest densities of spawning striped bass or changing release strategies (i.e. “barging” smolts downstream, e.g. Rechisky 2012). Additionally, the relative success of Gaspereau River smolts may provide justification for focusing conservation efforts on this population rather than those facing higher initial mortality rates.

Identifying the factors that have contributed to the poor marine survival of Atlantic salmon over the last two decades has been the focus of significant scientific investigation. While mortality in North American salmon populations is thought to be highest before the first winter at sea (Hansen and Quinn 1998), more exact estimates of the timing and identification of the source of this mortality has yet to be identified. The results of this study do not identify a source of mortality sufficiently large to account for observed declines; however, we do narrow the window when the most influential mortality is expected to occur.

Table 5.1 – Summary of acoustic telemetry tag and receiver deployments in the Gaspereau and Stewiacke rivers in 2008 and 2011.

River	Year	Release	Release Date	Number Released	Tag Model	Mean FL \pm sd (mm)	Receivers Deployed
Gaspereau	2011	2	17-May	20	V9-6L	193 \pm 8	7
Stewiacke	2011	1	25-May	12	V9-6L	147 \pm 6	8
Stewiacke	2011	2	27-May	15	V9-6L	150 \pm 8	8
Stewiacke	2008	1	23-May	19	V9-6L	n/a	6
Stewiacke	2008	2	30-May	22	V9-6L	n/a	6
Stewiacke	2008	3	06-Jun	15	V9-6L	168 \pm 11	6
Stewiacke	2008	4	13-Jun	10	V9-6L	164 \pm 8	6

Note: Hatchery-origin smolt tagged and released into each inner Bay of Fundy river by year and release group. Receivers deployed represents only those in the river. Receivers in Minas Basin were deployed only in 2011. *For Stewiacke River smolts, the mouth of the river was the mouth of the Shubenacadie River.

Table 5.2- Patterns of tag detection along the migration milestones; from release to the Minas Passage.

River	Year	Release	No. Released	No. with>1 total detections	Number detected at:				
					HoT	Confluence of Stewiacke and Shubenacadie Rivers	Mouth of estuary	Minas Basin	Minas Passage
Gaspereau	2011	2	20	15	14	<i>n/a</i>	8	5 (0) ¹	7 (0) ¹
Stewiacke	2011	1	12	11	11	6	1	2 (1) ¹	1 (0) ¹
Stewiacke	2011	2	15	11	11	6	5	4 (2) ¹	1 (1) ¹
Stewiacke	2008	1	19	17	17	16	7	<i>n/a</i>	<i>n/a</i>
Stewiacke	2008	2	22	19	19	16	12	<i>n/a</i>	<i>n/a</i>
Stewiacke	2008	3	15	3	3	1	0	<i>n/a</i>	<i>n/a</i>
Stewiacke	2008	4	10	2	2	1	0	<i>n/a</i>	<i>n/a</i>

¹(number of tags not detected at river mouth). **Note:** Tag presence was based on successful detection or by inferring presence based on detections downstream of the milestone. For salmon exhibiting reversal behaviour, milestones include detection during the final seaward descent. HoT = head of tide.

Table 5.3 – Summaries of migration metrics used in the Stewiacke River 2008 cluster analysis for each of the three major clusters.

Metric	Cluster 1	Cluster 2	Cluster 3
Total Displacement (km)	40.3 (14.3 - 124.5)	85.2 (18.3 - 235.9)	189.7 (59.8 - 391.0)
Total Time Lapse (days)	6.8 (2.7 - 20.3)	20.1 (11.5 - 30.7)	21.2 (8.0 - 29.7)
Total Detections	65.5 (8 - 1487)	1175.0 (498 - 3193)	936.5 (456 - 1998)
Total Days with Detections	3 (2 - 8)	16 (8 - 22)	15 (8 - 26)
Total Number of Reversals	0.5 (0 - 5)	12 (3 - 25)	10.5 (8 - 32)
ToSG (days)	0.2 (0.8 - 6.1)	10.3 (<0.1 - 18.1)	10.6 (1.5 - 22.6)
Total Detections on receiver SH.8 (upper Shubenacadie)	0 (0 - 124)	196 (0 - 1999)	326 (0 - 2283)
Mean Upstream Speed (m/s)	0.0 (0.0 - 1.8)	0.3 (0.1 - 0.8)	1.2 (0.2 - 3.2)
Max Upstream Speed (m/s)	0.0 (0.0 - 4.8)	1.0 (0.2 - 3.4)	5.1 (0.4 - 19.1)
Mean Downstream Speed (m/s)	0.4 (0.1 - 0.9)	0.5 (0.2 - 1.6)	1.2 (0.5 - 2.3)
Max Downstream Speed (m/s)	1.3 (0.1 - 2.5)	1.5 (0.3 - 11.4)	7.0 (3.8 - 18.1)

Note: Cluster 3 contains primarily Atlantic salmon smolts, cluster 2 contains primarily striped bass but also three salmon , and cluster 1 contains exclusively striped bass. Values represent the median (range) of each individual tag within each cluster, regardless of species. ToSG = Time on spawning ground. Clusters are reported in order they appear in global model, from left to right.

Table 5.4 - Summary of sensitivity analysis for the Stewiacke River 2011 cluster analysis.

Salmon ID	Exited mouth¹?	Global	Subset #1	Subset #2	Subset #3	Subset #4
S 01	No					
S 02	No					
S 03	No			P		P
S 04	No			P		P
S 05	No					
S 06	Exit					
S 07	No					
S 08	No			P		P
S 09	No					
S 10	No					
S 11	Exit (ND) ²	P	P	P	P	P
S 12	Exit	P	P	P	P	P
S 13	Exit					
S 14	Exit	P	P	P	P	P
S 15	No	P	P	P	P	P
S 16	Exit					
S 17	Exit (ND) ²			P		P
S 18	No	P	P	P	P	P
S 19	No	P	P	P	P	P
S 20	No					
S 21	No					
S 22	Exit					
Total assigned as predated		6 of 22	6 of 22	10 of 22	6 of 22	10 of 22
Estimated predation rate		27.3%	27.3%	45.5%	27.3%	45.5%
No. smolts to reassign from exited to predated		2 of 8	2 of 8	2 of 8	2 of 8	2 of 8
Estimated survival rate		18.2%	18.2%	18.2%	18.2%	18.2%

¹Mouth of Shubenacadie River estuary. ²(ND) = Not detected at mouth of Shubenacadie River estuary. **Note:** The cluster analysis was run using all ten parameters (global model) and four additional subsets of the data; subset #1 (all parameters less the total time on spawning grounds), subset #2 (all parameters less the total number of reversals and total displacement), subset #3 (all parameters less the four speed metrics), and subset #4 (all parameters less the total number of detections and the total number of days with detections). For each set of the input parameters, the assigned fate for each salmon smolt tag is shown with those tags identified as suspected predation victims denoted by “P”.

The total estimates of predation rates and cluster analysis-adjusted ratio-based survival are provided at the bottom.

Table 5.5 - Summaries of migration metrics used in the Stewiacke River 2011 cluster analysis for each of the four major clusters.

Metric	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Total Displacement (km)	201.2 (180.0 - 229.5)	19 (5.6 - 43.7)	85.6 (49.5 - 136.7)	42.4 (22.3 - 71.3)
Total Time Lapse (days)	34.4 (30.0 - 40.1)	8.1 (5.4 - 12.6)	13.7 (8.7 - 20.9)	7.4 (4.2 - 19.2)
Total Detections	5465.7 (1333 - 11546)	209.3 (97 - 369)	1430.8 (591 - 3854)	557.7 (177 - 1120)
Total Days with Detections	27.3 (21 - 34)	4.4 (3 - 6)	12.8 (10 - 21)	5.1 (3 - 7)
Total Number of Reversals	32.7 (28 - 42)	0.3 (0 - 1)	14.4 (8 - 19)	4.4 (1 - 8)
ToSG (days)	18.2 (7.0 - 32.0)	0.8 (0.0 - 2.1)	8.7 (3.3 - 13.9)	2.5 (0.3 - 4.7)
Mean Upstream Speed (m/s)	0.7 (0.5 - 1.0)	0.1 (0.0 - 0.4)	0.6 (0.3 - 0.7)	0.8 (0.3 - 1.4)
Max Upstream Speed (m/s)	1.7 (1.6 - 1.8)	0.1 (0.0 - 0.4)	1.1 (0.8 - 1.6)	1.1 (0.5 - 1.7)
Mean Downstream Speed (m/s)	0.6 (0.5 - 0.6)	0.3 (<0.1 - 0.5)	0.3 (0.2 - 0.4)	0.4 (0.2 - 0.6)
Max Downstream Speed (m/s)	4.0 (1.3 - 6.7)	0.7 (<0.1 - 1.6)	1.1 (0.7 - 1.6)	1.2 (0.6 - 2.1)

Note: Value represent the median (sd) of each individual tag within each cluster, regardless of species. ToSG = Time on spawning ground. Clusters are reported in order they appear in global model, from left to right.

Table 5.6 - Stewiacke River 2008 contingency tables for the probabilities of being; detected at the mouth (of the estuary) and either re-assigned as within a striped bass (P_{DR}) or remain assigned as a survivor (P_{DS}), or being undetected at the mouth and either re-assigned as within a striped bass (P_{UR}) or remain assigned as a survivor (P_{US}).

	Re-assigned as within a striped bass	Assigned as a survivor	SUM
Detected	$P_{DR} = 0.073$	$P_{DS} = 0.390$	$P_D = 0.463$
Undetected	$P_{UR} = 0.009$	$P_{US} = 0.046$	$P_U = 0.055$
SUM		$P_S = 0.436$	

Note: The overall probability of being undetected (P_U) is the difference between the cumulative Cormack-Jolly-Seber (CJS) mark-recapture model and the ratio-based survival estimate. The true probability of surviving (P_S) to the mouth of the estuary whether detected or not, and after considering the potential for predation by striped bass is the union of results from the CJS model and cluster analyses.

Table 5.7 - Stewiacke River 2011 contingency tables for the probabilities of being; detected at the mouth (of the estuary) and either re-assigned as within a striped bass (P_{DR}) or remain assigned as a survivor (P_{DS}), or being undetected at the mouth and either re-assigned as within a striped bass (P_{UR}) or remain assigned as a survivor (P_{US}).

	Re-assigned as within a striped bass	Assigned as a survivor	Sum
Detected	$P_{DR} = 0.091$	$P_{DS} = 0.182$	$P_D = 0.273$
Undetected	$P_{UR} = 0.030$	$P_{US} = 0.061$	$P_U = 0.091$
<i>SUM</i>		$P_S = 0.243$	

Note: The overall probability of being undetected (P_U) is the difference between the cumulative Cormack-Jolly-Seber (CJS) mark-recapture model and the ratio-based survival estimate. The true probability of surviving (P_S) to the mouth of the estuary whether detected or not, and after considering the potential for predation by striped bass is the union of results from the CJS model and cluster analyses.

Table 5.8– Summary of survival and predation rate estimates for each analytical method.

River	Year	Parameter	Ratio method	CJS	Cluster analysis- adjusted ratio ¹	Cluster analysis - adjusted CJS*
Gaspereau	2011	Survival	53.3%	54.0%	<i>n/a</i>	<i>n/a</i>
Stewiacke	2008	Survival	46.3%	51.8%	39.0%	43.6%
Stewiacke	2011	Survival	27.3% (36.4%) ¹	36.4%	27.3%	24.3%
Stewiacke	2008	Predation rate	<i>n/a</i>	<i>n/a</i>	7.3%	<i>n/a</i>
Stewiacke	2011	Predation rate	<i>n/a</i>	<i>n/a</i>	27.3%	<i>n/a</i>

¹(Uses ratio-based estimate after adjusting for ancillary data provided by Minas Basin receivers) ²(Estimate in parentheses is the ratio-based estimate after adjusting for ancillary data provided by Minas Basin receivers). **Note:** Survival is estimated to the seaward extent of estuaries of each river. CJS = Cormack-Jolly-Seber mark recapture model. * Cluster results represent the full model which used all movement parameters.

Table 5.9 – Summary of estimates for the estuarine survival of Atlantic salmon smolts in rivers of the Bay of Fundy, Gulf of Maine and Nova Scotia Southern Upland.

River	Year of study	Fish origin	Discount handling mortalities ?	Method	Estimated survival to mouth of estuary	Source
Stewiacke	2008	H	Yes	CJS-Cluster	43.60%	<i>This Study</i>
Stewiacke	2011	H	Yes	CJS-Cluster	24.30%	<i>This Study</i>
Gaspereau	2011	H	Yes	CJS ¹	54.00%	<i>This Study</i>
<i>Other Studies on the Stewiacke or Gaspereau Rivers</i>						
Gaspereau	2002	H	Yes	CJS ²	69%	Lacroix 2008
Stewiacke	2002	H	Yes	CJS ²	80% ³	Lacroix 2008
<i>Other BoF Rivers</i>						
Upper Salmon	2001-2002	W and H	Yes	CJS ²	97-100%	Lacroix 2008
Big Salmon	2001-2002	W and H	Yes	CJS ²	78-96%	Lacroix 2008
Nashwaak	2002	W and H	Yes	CJS ²	56-59%	Lacroix 2008
St. John	2001	H	Yes	CJS ²	44-55%	Lacroix 2008
<i>Southern Upland Rivers</i>						
Lahave	2010	W	Yes	CJS ⁴	85%	Halfyard et al. 2013
Gold	2010	W	Yes	CJS ⁴	89%	Halfyard et al. 2013
West, Sheet Harbour	2008-2010	W	Yes	Known-fate ⁴	54-74%	Halfyard et al. 2013
St. Mary's	2010	W	Yes	Known-fate ⁴	83%	Halfyard et al. 2013
<i>Gulf of Maine Rivers</i>						
Narraguagus (ME)	1997-1999	W	No	CJS ¹	60-75%	Kocik et al. 2009
Narraguagus (ME)	2002-2004	W	No	CJS ¹	68-74%	Kocik et al. 2009

¹CJS estimates - not accounting for predation. ²CJS estimates, estimated from Fig. 7, excluding handling mortalities. ³Receiver location at mouth of Shubenacadie estuary was upstream from location used in this study. ⁴Halfyard et al. (2013) only report standardized survival (i.e. S per km); these estimates are the cumulative estimates to the mouth of the estuary, not the open ocean. **Note:** In all cases, survival was estimated to the

seaward extent of the estuary only. Only survival estimates provided in this study (excluding Gaspereau River 2011) account for the confounding effects of predation by fishes. Survival estimates were from the most upstream receiver in this study (Stewiacke R. = -1.7km, Gaspereau R. = 6.2km), and some rivers reported by Lacroix (2008), but was from the site of release in all other estimates.

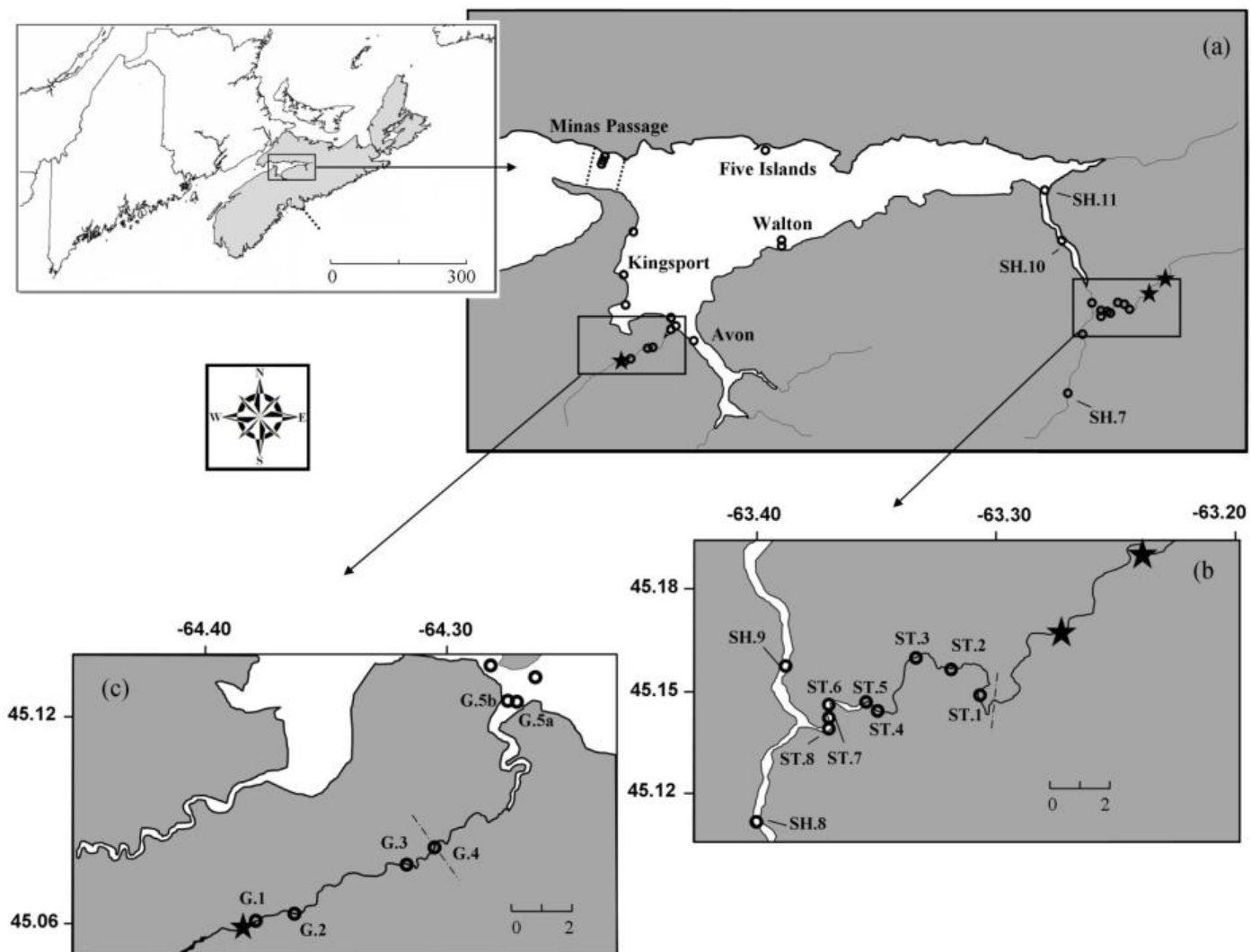


Figure 5.1 - Map of the Minas Basin with the inner Bay of Fundy (a), the Stewiacke River estuary (b) and the Gaspereau River estuary (c) in Nova Scotia, Canada, the location of acoustic receivers (open circles) and release sites (stars). Also shown are the receiver arrays at Halifax and within the Minas Passage (dotted line) and the head of tide (dashed line) in each river. All Minas Basin receivers, and those in the Gaspereau River were deployed in 2011 only. Stewiacke River receiver deployments were as follows: (2008) = ST.2, ST.3, ST.7, SH.9, SH.10, SH.11, plus SH.7 and SH.8. (2011) = ST.1, ST.3, ST.4, ST.5, ST.6, ST.8, SH.9 and SH.11.

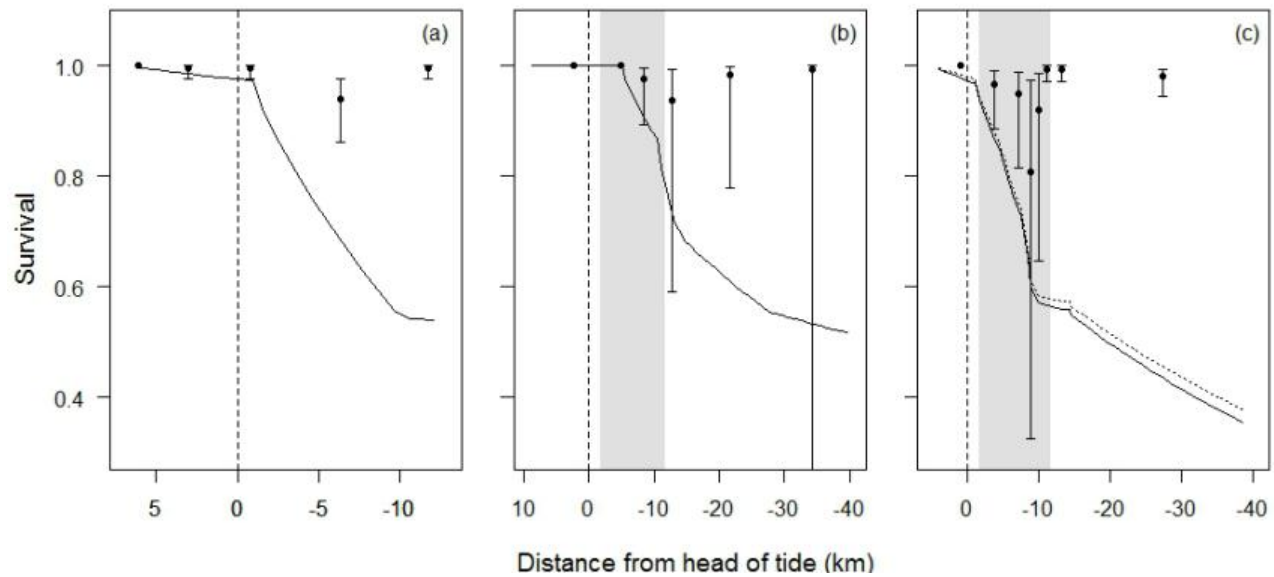


Figure 5.2 – Estimated survival in the Gaspereau River 2011 (a), and Stewiacke River 2008 (b) and 2011 (c). Cumulative survival (solid line) and mean (\pm 95% confidence intervals) standardized survival estimates (S/km, solid circle) as a function of distance from the head of tide (km). In panel (c), the solid line denotes the cumulative survival of release group 1 (25th of May), and the dotted line denotes the cumulative survival of salmon in release group 2 (27th of May). The approximate area of striped bass spawning grounds is denoted by grey shading. Head of tide indicated by the vertical dashed line.

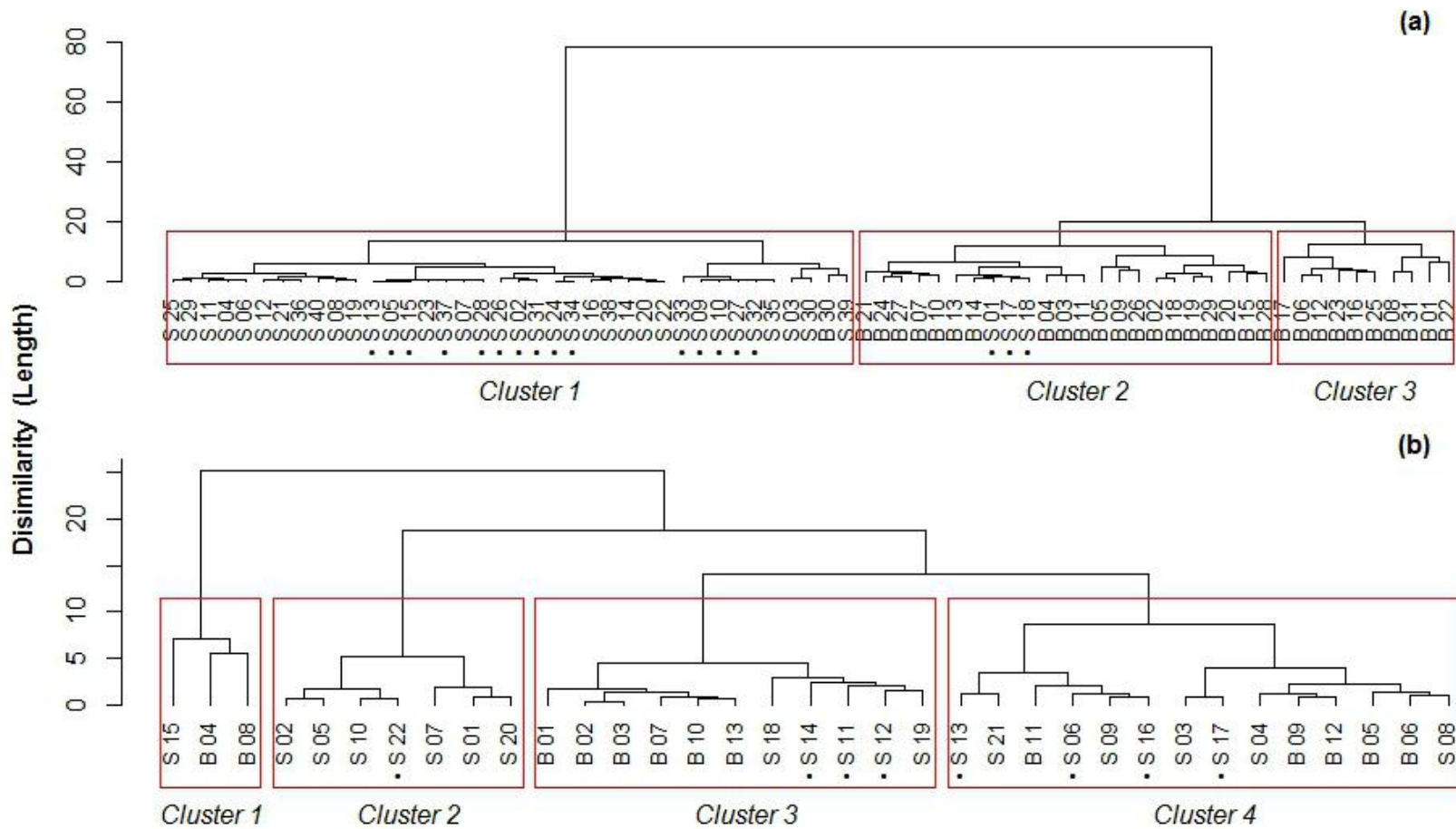


Figure 5.3 – Results of hierarchical clustering of Stewiacke River 2008 (a) and 2011 (b) data. Cluster names are nominal (i.e. do not

reflect the hierarchical order identified clusters). Species are shown as either Atlantic salmon smolts (S##) or striped bass (B##).

Smolts preceded by a solid circle indicate those that were detected 'exiting' the mouth of the estuary.

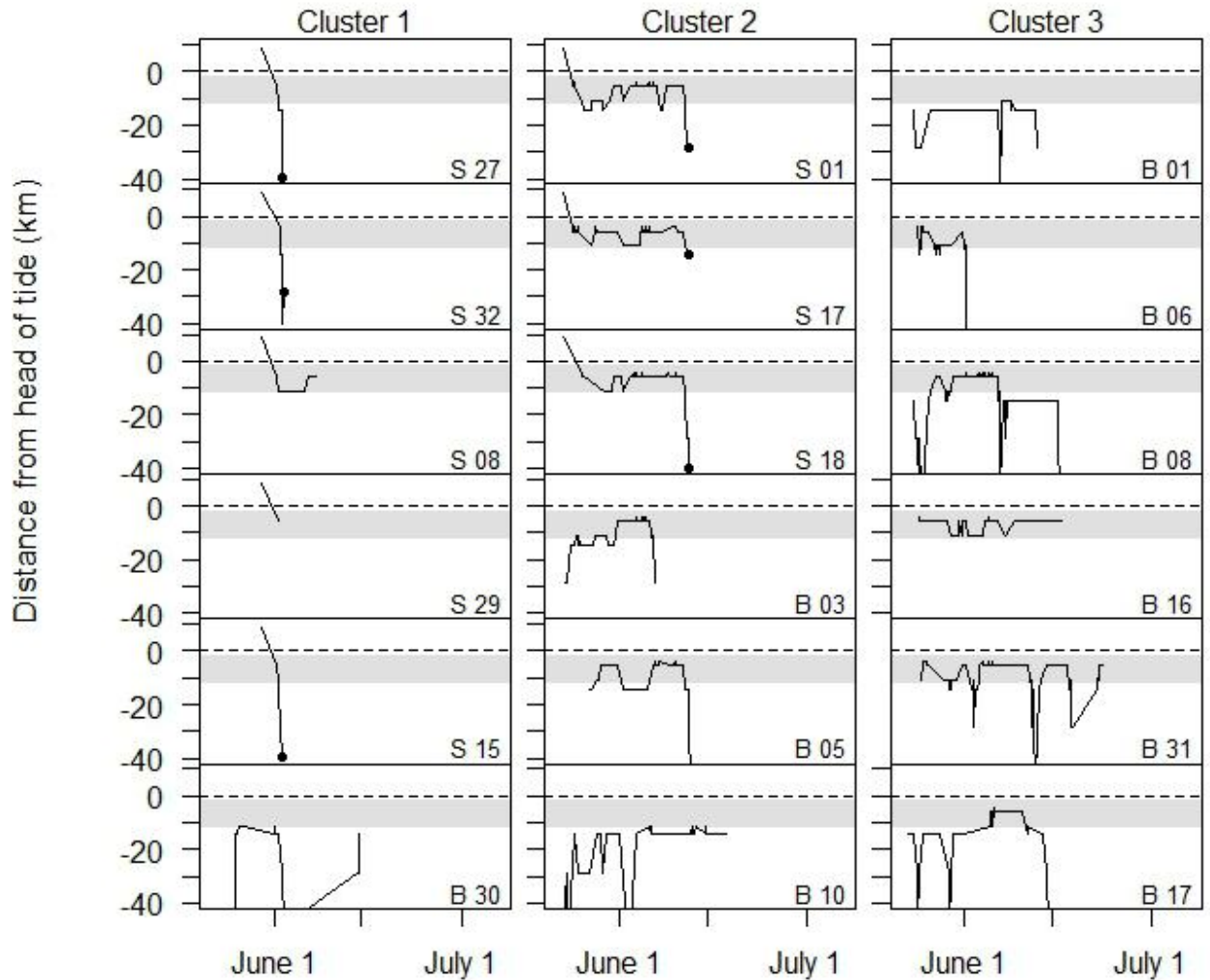


Figure 5.4 – Selected examples of estimated tag movements within the lower Stewiacke River, its estuary and the lower Shubenacadie estuary in 2008. All specimens for rare species in each cluster (e.g. ≤ 3) are shown, otherwise tags were randomly selected using a random number generator. Movement is described the distance from the head-of-tide (km) in the Stewiacke River for tags placed in salmon smolts (S ##) and striped bass (B ##). Solid circles at the end of tracks indicate when a tag was detected ‘exiting’ the mouth of the estuary. Columns represent each cluster from left (cluster 1) to right (cluster 3) in Figure 4. The dashed horizontal line is the head-of-tide and the shaded band represents the suspected spawning grounds of striped bass.

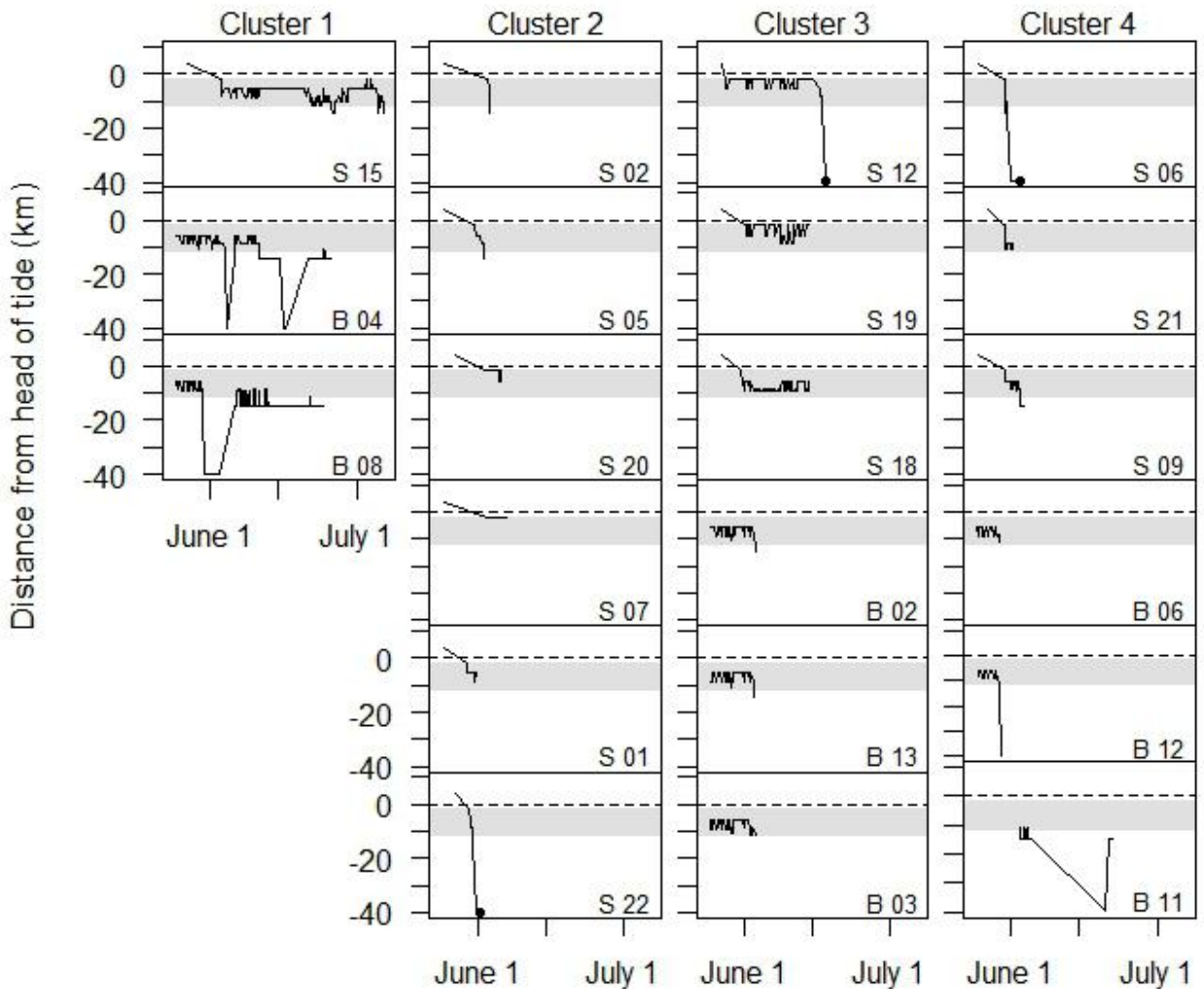


Figure 5.5 – Selected examples of estimated tag movements within the lower Stewiacke River, its estuary and the lower Shubenacadie estuary in 2011. All specimens for rare species in each cluster (e.g. ≤ 3) are shown, otherwise tags were randomly selected using a random number generator. Movement is described the distance from the head-of-tide (km) in the Stewiacke River for tags placed in salmon smolts (S ##) and striped bass (B ##). Solid circles at the end of tracks indicate when a tag was detected ‘exiting’ the mouth of the estuary. Columns represent each cluster from left (cluster 1) to right (cluster 4) in

Figure 4. The dashed horizontal line is the head-of-tide and the shaded band represents the suspected spawning grounds of striped bass.

CHAPTER 6: DISCUSSION AND CONCLUSIONS

The overall goal of this thesis was to better understand the factors affecting the survival of Atlantic salmon during the early marine phase of their life history. Atlantic salmon populations have been subjected to exploitation, habitat degradation and habitat fragmentation for centuries (WWF 2001), however, widespread poor marine survival since approximately 1990 (Potter et al. 2003, Chaput 2012) has led to declining or extirpated populations across the Atlantic salmon's distribution (Hutchinson and Mills 2000, Hawkins 2000, Gibson et al. 2009; 2011). This thesis contributes to our knowledge of Atlantic salmon survival during the early marine phase by using acoustic telemetry to estimate the survival of Atlantic salmon smolts and postsmolts in estuarine and coastal habitats, identifying potential causes of estuarine / coastal mortality via acoustic telemetry, and addressing the limitations of acoustic telemetry for estimating fish survival using modelling-based approaches.

6.1. OVERVIEW

The first research objective of this thesis was to review the available literature to identify potential mechanisms responsible for recent poor marine survival and identify when important periods during the marine phase of salmon are likely to occur. In chapter two, we reviewed and synthesized the current body of literature on the marine survival of Atlantic salmon. This review identified several important generalities: shifts in the marine survival of Atlantic salmon occurred abruptly around 1990, survival shifts were associated with widespread ecosystem regime shifts in the North Atlantic Ocean,

populations throughout the salmon's distribution experienced survival shifts, and survival shifts occurred for several life histories.

This literature review was informative for several reasons, most notably to (1) narrow the focus of the research by identifying the early portion of the marine phase, including estuaries and coastal areas, where postsmolt mortality may be elevated, and (2) by directing research effort toward identifying mortality vectors associated with predation. It is widely suspected that predation is an important source of marine mortality (e.g. Thompson and MacKay 1999, Cairns and Reddin 2000, Montevecchi et al. 2002, Montevecchi and Cairns 2007), however, studies that have formally examined drivers of Atlantic salmon marine survival have focused on climate or prey resources only (e.g. Beaugrand and Reid 2003; 2012, Mills et al. 2013), and not predation. Thus, this review addressed the largely neglected link between ecosystem regime shift and Atlantic salmon survival. The research conducted in chapters three through five were guided by these findings.

The second research objective of this thesis was to estimate the survival of postsmolts in selected estuaries and coastal habitats using acoustic telemetry. To meet this research objective, we examined the behaviour and survival of Atlantic salmon smolts from four rivers in Nova Scotia's Southern Upland (SU) and two rivers of the inner Bay of Fundy (iBoF) using acoustic telemetry.

The survival estimates reported in this thesis are important because they divide the marine phase into two periods; an early period spanning < 1 month during the initial movement to the ocean, and the remaining 12 (for 1SW) to 28 (for 2SW) months at sea.

By estimating survival during the earliest portion of the marine phase, our knowledge of marine mortality can be partitioned, thus partially refining the coarse temporal resolution provided by current marine return rate data (e.g. Crozier and Kennedy 1999, Freidland et al. 2000, Peyronnet et al. 2008).

The third research objective of this thesis was to test the potential mortality mechanisms identified in the literature review. To meet this research objective, we used four approaches related to acoustic telemetry. First, we reported field studies of mortality based on patterns of tag ‘losses’, by combining passive and active acoustic telemetry. To my knowledge, no other acoustic telemetry studies have used a similar approach to quantifying avian predation; however, radio telemetry (which transmits signals through air) has been used to assess avian predation (Jepsen et al. 1998, Dieperink et al. 2002). Other authors have noted the general “disappearance” of telemetry tags during their studies and suggested it could be related to natural mortality (e.g. Hedger et al. 2008, Moland and Moland 2011), but they did not provide evidence to back up the speculations and did not extend the findings to estimate population-level removal rates. Future use of this method should employ careful range and efficiency testing (similar to what was reported in this thesis).

Potential mortality vectors were also identified by identifying covariates of survival in Cormack-Jolly-Seber (CJS) mark-recapture models. Both positive and negative correlations between survival and body (fork) length were observed. Positive size-selective survival is consistent with predation (e.g. Blaxter 1986, Miller et al. 1988, Cowan et al. 1996, Sogard 1997), while the cause of negative size-selective survival is

unknown, but may be related to damage from the duration of freshwater exposure to sub-lethal acidification and aluminum at my study sites (e.g., Staurnes et al. 1996, Monette et al. 2008, Kroglund et al. 2012, McCormick et al. 2012), and a subsequent increased susceptibility to predation (Järvi 1989, Handeland 1996, Kroglund et al. 2007) – the “maladaptive anti-predator behaviour” hypothesis (Järvi 1989). These divergent body size – survival correlations highlight the potentially diverse factors affecting salmon in these areas.

Insights on potential mortality vectors were also investigated by modelling the relationship between migratory behaviour and survival. Most notably, there was evidence of a quadratic relationship between residency and survival for populations where survival was strongly correlated with body-size. Such a relationship may signify a trade-off between the threat of predation (that warrants exiting the area rapidly) and the physiological demand of osmoregulation (that warrants slowly adjusting to the marine environment). This result is novel and illustrates how multiple stressors may act simultaneously to impact the estuarine survival of Atlantic salmon postsmolts.

Finally, a novel cluster-analysis modelling approach was used in an attempt to identify predation events where tagged iBoF smolts were consumed by predatory striped bass; a widely suspected predator of out-migrating salmon smolts and postsmolts (Blackwell and Jaunes 1998, Beland et al. 2001, Grout 2006). A current gap in our understanding of striped bass – salmon interaction is our inability to quantify the population-level impact of predation (i.e. predation rates). The cluster analysis approach provided indirect evidence that predation by striped bass was occurring, and attempted to

quantify the population-level predation rate. The results presented in this thesis confirmed that striped bass are important predators of Atlantic salmon smolts/ postsmolts at our study site and illustrates the need to consider this and other predators in Atlantic salmon conservation programs. This information may prove useful for tailoring release strategies of supplemental hatchery-reared fish to reduce predation (e.g. Karam et al. 2008), such as those used in the live gene banking program operated by Fisheries and Oceans Canada (Gibson et al. 2004).

The final research objective of this thesis was to develop methods to address the major limitations to estimating survival using acoustic telemetry. The novel cluster-analysis model contributed here. One of the most severe limitations of acoustic telemetry is the inability to identify precisely when tagged animals are consumed by a predator. Acoustic tags continue to transmit while in the stomachs of predators (Beland et al. 2008, Thorstad et al. 2012), potentially leading to erroneous interpretation of telemetry data and the overestimation of survival if the predators migrate outside the study area. To date, estimates of predation on salmon by piscivorous fishes has relied on acoustic tags with ancillary sensor data such as depth or temperature (Thorstad et al. 2011a) or other telemetry technologies with depth sensors (Dieperink et al. 2002, Béguer-Pon et al. 2012, Lacroix 2014, Wahlberg et al. *In Press*). Sensor tags are larger than non-sensor tags and are therefore can only be used on large salmon smolts (e.g. > 22cm) which precludes most wild populations. A benefit of the cluster-analysis based approach is that non-sensor tags can be used to identify predation in smaller fish.

The limitations of the cluster-analysis based approach are important to consider in its future use, including; the need for a “linear” study site (e.g. river or narrow estuary where fish migration is bounded by land on two sides), the need to tag potential predators, identification *a priori* of migration metrics that clearly differentiate between predator and prey, and the subjective nature of interpretation of some cluster results. The development of state-space Bayesian models to discern patterns in apparent migratory behaviour may address some of these limitations, however, modelling approaches are likely to remain limited by assumptions, thus the continued development of telemetry technologies is important. In particular, the miniaturization of sensor tags and the development of tags that definitively identify predation events through the use of novel sensors is needed.

In an effort to address another major limitation of acoustic telemetry, detection efficiency, we used the CJS models to estimate this parameter. These mark-recapture models greatly improved the accuracy of survival estimates, particularly for iBoF rivers where extreme tides had a significant influence on detection efficiency, further highlighting the importance of considering gear performance in survival estimates. CJS models are easily implemented and where experimental designs meet their assumptions should (nearly always) be used when estimating survival via acoustic telemetry.

In this thesis, several methods were used to estimate survival rates. A major advantage of the mark-recapture approaches used in chapters 4 and 5 are that standard errors are estimated for each parameter estimate (e.g. survival between individual receivers). However, the standard errors of the individual parameter estimates are not

easily carried forward to the estimate of cumulative survival. In the case of the ratio-based survival estimates (chapters 2 and 5), standard errors could be calculated by assuming a binomial sampling error, however this approach would be questionable given the evidence for over-dispersion provided in the CJS analyses. Standard errors for survival estimates from the cluster analyses cannot be estimated because of the need to assign the fate of salmon in each cluster when interpreting the results. Improved methods for assessing parameter uncertainty associated with telemetry-based survival estimates would allow for better evaluation of the statistical significance of the results of these types of studies, including statistical comparison of survival estimates both within and among populations, and is recommended as a topic of future research.

A recurring theme throughout this thesis is that of variability and diversity. There is little question that the common trend for many Atlantic salmon stocks is an abrupt shift toward reduced marine return rates circa 1990 (Beaugrand and Reid 2003; 2012, Mills et al. 2013). However, as evidenced in the literature review (chapter 2), there was also evidence that not all populations were impacted equally. For example, the smolt-adult return rate declines were less pronounced for northern populations with some actually experiencing increased marine return rates. Return rates declined for repeat spawners in some populations, whereas in others they increased. Interestingly, shifts in the return rates of repeat spawners generally occurred later (ca. mid- to late-1990s) than smolt-to-adult (virgin) return rates (circa 1990). The timing and magnitude of return rates shifts also appeared to differ between wild- and hatchery-origin salmon. Finally, declines were more pronounced in 2SW salmon than 1SW salmon. Additional evidence of this variability is provided by (even visual) examination of reported marine return rates across North

America and Europe (ICES 2013). Here, it is apparent that not all populations experienced a rapid shift at the same time, of the same magnitude or, even, with the same outcome (i.e. increasing or decreasing).

This significant variability in the timing and magnitude of return rate shifts challenges the current paradigm of declining marine survival of Atlantic salmon, where all populations and life stages are thought to experience common threats in a common marine environment. The results presented in chapter two suggest that variable marine return rates among life history groups (e.g. SW vs 2SW virgin salmon and consecutive vs. alternate repeat spawning salmon) may be a result of these groups occupying different marine habitats. The marine distribution of Atlantic salmon is relatively unknown (Jacobsen et al. 2001), however, 1SW and consecutive spawning salmon likely occupy different ocean habitat relative to 2SW and alternative repeat spawners (Jonsson and Jonsson 2004, Chaput and Benoit 2012). Likewise, variability in the general timing of shifts between virgin and repeat spawners may be related to differences in body size, and trophic position of these life stages. Here, younger and smaller salmon are subjected to exorbitant predation pressures that overshadow other factors that impact marine survival whereas the older and larger repeat spawners are less impacted by predation, and therefore other factors impacting survival (e.g. prey availability or quality) may be more important.

At a population-level, variable marine return rates, and the estimates of estuarine / coastal survival presented in the research chapters, may be related to local estuarine and ocean conditions. The estuarine survival of Atlantic salmon was highly variable among

regions, rivers and years and may reflect variability in population-specific traits (e.g. run timing), physical habitat characteristics (e.g. abrupt vs. elongated estuaries), pollution (e.g. acidification), predation fields, or inter-annual hydro-climatic differences. These differences may also explain the observation of variable migration behaviour where some populations spend extended time in inner estuary habitats or make repeated migration reversals while others transit estuaries rapidly and without migration reversals.

At a smaller scale, survival in some rivers was highly habitat-dependent with poor survival that was highly size-selective in the inner portion of estuaries. By contrast, survival in other rivers was constant over time with no habitat effect and little evidence of size-selection. Finally, there was also evidence that the dominant mortality vectors may be similarly variable at the regional, river and habitat scale. For example, avian predation appears to be the most important mortality vector in the SU with individual salmon predation risk potentially elevated by exposure to sub-lethal acidic conditions. Alternatively, striped bass appear to be an important predator in iBoF estuaries, particularly the Stewiacke River where a large striped bass spawning population exists.

Atlantic salmon populations exhibit significant life-history (Saunders and Schom 1985, Hutchings and Jones 1998), genetic (Verspoor 1997, King et al. 2001, Dionne et al. 2008) and phenotypic plasticity (Riddell and Leggett, 1981, Claytor et al. 1991), and the marine migration of Atlantic salmon is also variable (Reddin 1988, Hansen and Quinn 1998). Therefore it may be reasonable to expect that estuarine and marine survival is similarly diverse. As a result, the effect of estuarine and coastal survival on marine return rates and the eventual effect on population viability and persistence may exhibit similar

variability. Conservation planning needs to consider the potential for diverse trends and drivers of marine survival that may occur at the population-level scale.

6.2. DOES ESTUARINE AND COASTAL MORTALITY MATTER?

With the ability to quantitatively estimate salmon survival through estuaries and coastal areas, the challenge is to determine whether the mortality incurred during this initial phase is important; specifically whether it is sufficient to account for recent poor marine return rates. One approach to this challenge is to compare telemetry-based estimates of survival to known marine return rates; thus permitting an assessment of the importance of estuarine (and coastal) mortality relative to the mortality in the remaining marine phase.

Return rate data are limited for the study rivers, however, a time series is available for the Lahave River and St. Mary's River in the SU. Combined 1SW and 2SW return rates for the period 2000 to 2009 averaged 0.026 and 0.013 for the Lahave and St. Mary's Rivers, respectively (Gibson et al. 2009, Gibson and Bowlby 2013). Return rates for iBoF populations are limited to a few sporadic estimates in the Gaspereau and Big Salmon Rivers (e.g. Gibson et al. 2004). Relative to the combined return rates for 1SW and 2SW, the estimates of estuarine/ coastal mortality reported in this thesis account for only 8.4% (Lahave River), 9.0% (St. Mary's River) and 11.6% (Gaspereau River) of total marine mortality. This rate appears high relative to the short time that salmon occupy these habitats. The temporal period covered by the survival estimates reported in this thesis account for only 0.065 (1SW) and 0.035 (2SW) of the marine residency for SU

salmon and 0.021 (1SW) and 0.011 (2SW) of the marine residency for iBoF salmon assuming a marine residency of approximately 400 days and 750 days for virgin 1SW and 2SW salmon, respectively.

The expectation should be that marine mortality of Atlantic salmon is highest in estuaries and coastal environments. For example, the inverse-weight hypothesis (Doubleday 1979) posits that Atlantic salmon mortality varies inversely to the weight of the salmon. Under this hypothesis, postsmolts first entering the marine environment (e.g. estuaries and coastal areas) would be subject to the highest mortality rates. Further, this expectation for high mortality is logical as estuaries are transitional environments where Atlantic salmon adjust to the hyperosmotic marine environment; facing new predators, prey, habitats, and physiological challenges (McCormick et al. 1998, Weitkamp et al. 2014).

From a conservation standpoint, three management-relevant outcomes are possible when comparing estimates of estuarine / coastal mortality to mortality in the remaining marine phase; (1) estuarine/coastal mortality is sufficient to account for reduced marine return rates and thus should be the focus of mitigation, (2) estuarine/coastal mortality is insufficient to account for reduced marine return rates, however, mitigating this mortality would improve adult returns and possibly lead to viable populations, or (3) estuarine/coastal mortality is insufficient to account for reduced marine return rates and mitigating this mortality will have negligible effect on population viability.

As an exercise, it may be useful to examine the impact of improving estuarine / coastal survival (i.e. reducing mortality) on subsequent marine return rates. Survival rates, expressed as a proportion, are multiplicative (Ricker 1975). As such, return rates can be decomposed into two terms, one related to early (coastal/estuarine) survival , and one related to the remaining survival that occurs later in the marine residency of salmon (equation #1):

$$(1) \text{ Return Rate} = S_{\text{early}} * S_{\text{later}}$$

where increased early survival (e.g. as a result of conservation strategies), would lead to an increased return rate:

$$(2) \text{ Return Rate} = S_{\text{new.early}} * S_{\text{later}}$$

Finally, assuming that survival in the open ocean is independent of estuarine and coastal survival (i.e. survival in the open ocean is not density dependent; Jonsson et al. 1998, Jonsson and Jonsson 2004), the impact of increasing S_{early} on the subsequent return rates is as follows:

$$(3) \text{ Percent Increase of Return Rate} = \left[\frac{S_{\text{new.early}}}{S_{\text{early}}} - 1 \right] * 100$$

This brief set of calculations show that the impact of improved estuarine/coastal survival increases via a power function with decreasing S_{early} . As such, increasing S_{early} leads to a disproportionately large increase in return rates for populations where S_{early} is low and a disproportionately small increase in return rates for populations where S_{early} is high (Fig. 6.1).

Using the river-specific return rate data, eliminating all estuarine and coastal mortality (i.e. 100% survival) would increase return rates from 0.026 to 0.036 for the Lahave River population, from 0.013 to 0.019 for the St. Mary's Rivers population, and from 0.005 to 0.014 in the Gaspereau River. Historical return rates (1SW and 2SW combined) in the 1970s and 1980s were 0.084 to the Lahave River and 0.059 to the St. Mary's River in the SU (Gibson and Bowlby 2013), and likely were close to 0.060 for iBoF rivers during the late 1960s and early 1970s (Ritter 1989). In all cases, eliminating estuarine/coastal mortality would not produce return rates similar to pre-decline population dynamics (even before considering historical fishing mortality). This suggests that changes to estuarine and coastal mortality cannot be solely responsible for population declines, and that the highest mortality during the early portion of the marine phase rates must occur outside of estuaries and early coastal habitats.

In the case of the three study rivers where return rates data exist, reducing early marine mortality is not likely to have significant population-level effects. For example, Gibson and Bowlby (2013) used population viability modelling to simulate the effect of changing population dynamics for the Lahave River and St. Mary's River populations. They estimated that under current freshwater productivity scenarios, marine return rates as low as 0.044 and 0.022, respectively, would decrease the risk of extirpation to near zero. These return rates could not be achieved by reducing estuarine / coastal mortality. Similarly, Amiro (2003) estimated that iBoF populations would be close to viable at a marine return rate of 0.036. Removing 100% of estuarine mortality would generate return rates of 0.009 in the Gaspereau River and thus would not lead to viable iBoF populations or a reduced risk of extirpation.

The rivers where return rate data exist as also those rivers where smolts experience relatively high S_{early} , and thus it is unclear what impact S_{early} has on return rates in these populations with relatively poor S_{early} ; those expected to benefit the most from improved S_{early} (Fig. 6.1). Assessing the population-level impact of improving S_{early} is problematic for populations without return rate data and without population viability data. One approach is to assume that S_{later} is similar to other rivers in the region (e.g. intermediate to the Lahave and St. Mary's River in the SU and similar between the Stewiacke and Gaspereau River), and that these rivers differ only in their S_{early} . This assumes that salmon post-smolts in a common environment experience similar survival. Following this approach, elimination of estuarine / coastal mortality would generate return rates of between 0.019 and 0.035 in the Gold/ West Rivers and 0.009 in the Stewiacke River. However, by comparing S_{later} between the Lahave ($S_{\text{later}} = 0.308$) and St. Mary's Rivers ($S_{\text{later}} = 0.392$) it is apparent that S_{later} may vary and thus the assumption of similar S_{later} is questionable.

In summary, estuarine and coastal mortality is not likely sufficient to account solely for population declines. Conservation measures aimed at improving the estuarine and coastal survival of salmon are unlikely to elicit a significant population response for populations with high S_{early} (low mortality) and where return rates are currently monitored. In rivers where return rates are unmonitored and S_{early} is poor (high mortality), it is unclear if improving estuarine / coastal survival would be sufficient to reduce the risk of extirpation or elicit population recovery, however these population should, in theory, realize the largest benefit of such conservation actions. Paired with other conservation measures, such as improving freshwater productivity (e.g. via habitat enhancement, acid

mitigation), conservation efforts directed at improving estuarine /coastal survival in these populations should be considered, particularly given our inability to affect the marine survival of salmon in the open ocean.

6.3. MANAGEMENT IMPLICATIONS, FUTURE RESEARCH AND CONSERVATION PLANNING

In this thesis we found evidence that estuarine and early coastal mortality occurs at a relatively high rate and that predation is a significant mortality vector. The estuarine mortality rates described in this thesis were insufficient to account for declines in overall marine return rates; however, the results do not preclude some benefit from conservation efforts to improve estuarine / coastal survival, particularly for populations where this survival is currently low.

With a goal of reducing extinction risk, there are two basic policy approaches to affecting change; (1) a symptomatic approach, or (2) a systematic approach (Lessard et al. 2005). In the case of endangered Atlantic salmon, the symptomatic approach would directly address acute and known sources of mortality (e.g. predator removal, removal of dams) whereas a systematic approach would consider the entire ecosystem and affect change so that the ecosystem becomes more favorable for Atlantic salmon (e.g. increase the abundance of alternative prey available for potential salmon predators).

Following a symptomatic approach, efforts to reduce predation of Atlantic salmon postsmolts in SU estuaries could involve the removal (i.e. culling) of double crested cormorants, mergansers and other potential predators. Cormorant populations have been

previously subjected to culling as a management approach. For example, Bedard et al. (1997) described a four year cull of double crested cormorants (and the oiling of eggs) in the St. Lawrence River estuary that successfully reduced the cormorant population to a predetermined target abundance.

However, the effect of culling predators is rarely straight-forward nor easily predicted (Ward and Hvidsten 2011, Bowen and Lidgard 2011). Further, culling is not applicable to many predator populations of concern (e.g. loons, ospreys, eagles) and even intense programs often fail to meet project objectives due to the difficult logistics of predator control (Halfyard 2010). Finally, culling is not widely palatable to the general public, and discussion of culling frequently elicits significant public outcry (Bedard et al. 1995; 1997, Lessard et al. 2005). The philosophical and ethical aspects of controlling predator populations to aid endangered species would need to be fully explored prior to any culling program aimed at addressing the SU cormorant-salmon conflict.

An alternative to predator removals is sub-lethal harassment techniques where predators are displaced from sensitive areas during sensitive times. This approach has been used on the Narraguagus River (Maine, USA) where cormorants in the estuary were displaced by approaching them on foot or in a boat, using noise-making equipment or pyrotechnics (Hawkes et al. 2013). Using acoustic telemetry to assess these efforts, cormorant displacement was estimated to reduce the likelihood of predation by ca. 80-85%. Because salmon smolts in the SU and iBoF occupy estuaries for only a few weeks each spring, and estuaries are small relative to coastal or open ocean habitats, sub-lethal predator harassment appears to be a feasible, and potentially effective, conservation

option. Careful planning and monitoring should accompany any such effort to permit a thorough evaluation.

In the case of the iBoF, striped bass represent the most likely dominant mortality vector within the estuaries studied. Like iBoF Atlantic salmon, Bay of Fundy striped bass are also imperiled (designated as threatened, COSEWIC 2012) and thus predator control options are undesirable. A symptomatic approach to circumventing these efficient piscivores could be that of “barging” smolts past the areas of high predation. Barging involves capturing and transporting salmon smolts downriver in trucks or boats, and the practice is commonly used in the impounded rivers systems of western USA (Ward et al. 1997). Here, the survival of several Pacific salmon species has been improved by circumventing hydroelectric installations and non-native piscivorous fishes in impoundments (e.g. Ward et al. 1997, Congleton et al. 2000). Like any intervention requiring handling and (even temporary) containment, there are negative impacts; including stress (Maule et al. 1988, Congleton et al. 2000) and impacts to sensory systems (Halvorsen et al. 2009). This technique has not been previously used for Atlantic salmon, thus the efficacy of barging is unknown. Such an approach would require an annual investment of resources, careful planning and adequate program assessment.

Rather than focus on the acute issues impacting the estuarine survival of Atlantic salmon (e.g. predator abundance), ecosystem-based fisheries management (EBFM) would represent a systematic approach to creating healthier estuarine ecosystems – which would presumably be more favorable to Atlantic salmon. At its core, EBFM is “a new direction for fishery management, essentially reversing the order of management priorities to start

with the ecosystem rather than the target species.” (Pikitch et al. 2004). Under EBFM of estuaries, all species would be managed for their role in the greater ecosystem in addition to the fisheries or commercial industries they support. If EBFM produces an elevated abundance of other estuarine fishes, potential benefits to Atlantic salmon might include “predator swamping” (Ims 1990) which may reduce predation pressures on Atlantic salmon (Svenning et al. 2005). However, EBFM would require a significant shift in current management philosophies and likely significant time to implement.

It is clear that estuaries play an important ecological role in the marine phase of the Atlantic salmon. Estuaries are accessible, spatially explicit, and small in size relative to the open ocean. For all of these reasons, it is astounding that species recovery planning efforts have largely overlooked estuarine environments. For Atlantic salmon populations on the brink, estuarine mortality cannot continue to be ignored, and even marginal benefits of improving estuarine survival are worthwhile. A combination of symptomatic and systematic approaches are likely required for reducing the short-term immediate risk of extirpation faced by many populations and the long-term planning for naturally viable populations.

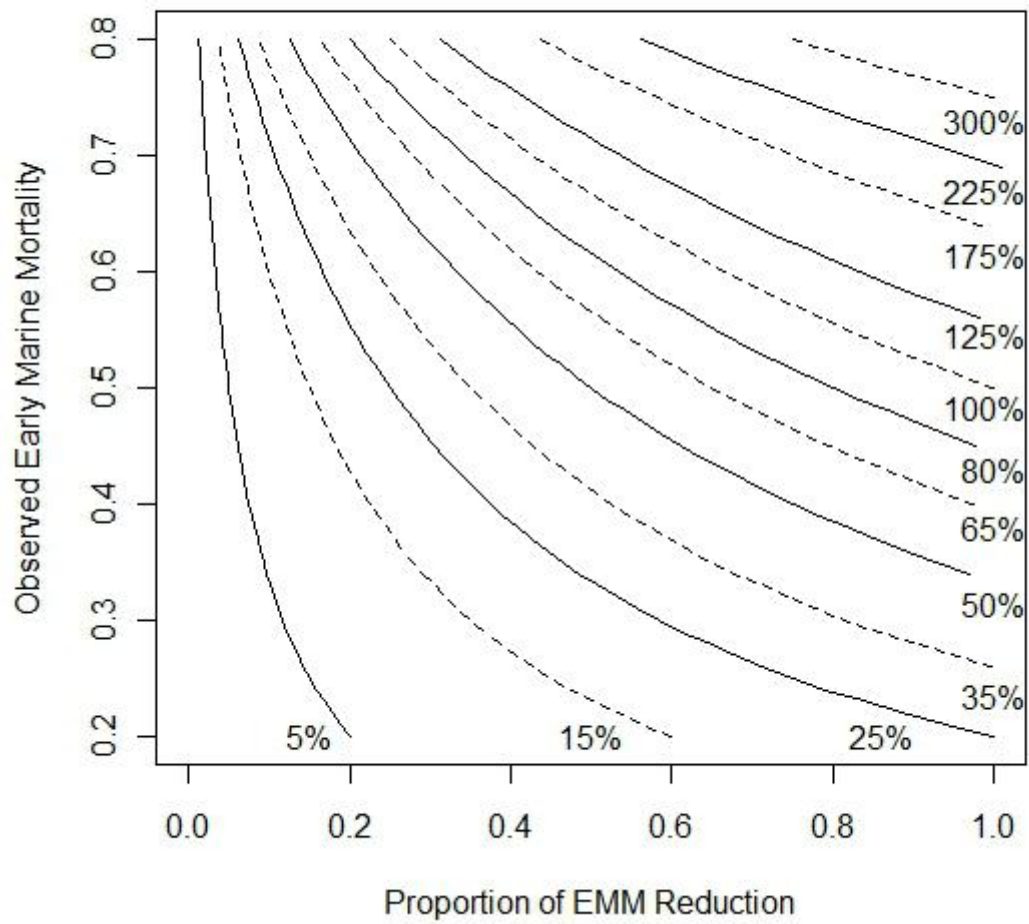


Figure 6.1 – Effect of reducing early marine mortality on overall smolt-to-spawner returns at varying rates of observed early marine mortality. Isobars indicate percentage increase in return rates.

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APPENDIX B: MARK-RECAPTURE MODEL POOLS FOR CHAPTER 4

Table B.1 – Pool of tested Cormack-Jolly-Seber models for Lahave River salmon smolt survival.

Model	AICc	Delta AICc	AICc weight	Number of Parameters	Deviance
S(FL) p(d), linear	147.155	0	0.620	14	117.671
S(FL) p(d), quadratic	149.195	2.041	0.224	15	117.493
S(TWR) p(d), linear	149.961	2.806	0.153	14	120.476

Note: Models estimate survival (S) and encounter probability (p, i.e. detection efficiency) and also incorporate fork length (L_F) or tag-to-body-weight ratio (TWR) as individual covariates. The shape of the assumed covariate-survival relationship is stated (either linear or quadratic) where applicable. Parameters were assumed to vary with distance from release (d, i.e. habitat-specific) or be consistent across all habitats (.). Models are ranked based on Akaike Information Criterion adjusted for small sample size. Only those models with an AICc weight greater than 0 are shown.

Table B.2 – Pool of tested Cormack-Jolly-Seber models for Gold River salmon smolt survival.

Model	AICc	Delta AICc	AICc weight	Number of Parameters	Deviance
S(DIST) p(DIST)	159.610	0	0.600	13	131.553
S(TWR + DIST) p(DIST), linear, diff INT common SLOPE	161.952	2.342	0.186	15	129.209
S(L _F + DIST) p(DIST), linear, diff INT common SLOPE	162.406	2.796	0.148	15	129.663
S(CON) p(DIST)	166.152	6.542	0.023	8	149.361
S(TWR) p(DIST), linear	166.561	6.951	0.019	9	147.566
S(L _F) p(DIST), linear	166.895	7.285	0.016	9	147.901

Note: Models estimate survival (S) and encounter probability (p, i.e. detection efficiency) and also incorporate fork length (L_F) or tag-to-body-weight ratio (TWR) as individual covariates. The shape of the assumed covariate-survival relationship is stated (either linear or quadratic) where applicable. Parameters were assumed to vary with distance from release (DIST, i.e. habitat-specific) or be consistent across all habitats (CON). Models are ranked based on Akaike Information Criterion adjusted for small sample size (AICc). Only those models with an AICc weight greater than 0.01 are shown.

Table B.3 – Pool of tested known-fate models for St. Mary’s River salmon smolt survival.

Model	AICc	Delta AICc	AICc weight	Number of Parameters	Deviance
S (REL)	93.062	0	0.772	2	89.015
S (REL + DIST)	97.130	4.068	0.101	11	74.074
S (DIST)	98.502	5.440	0.051	10	77.625
S (DIST * L _F), linear, diff. INTS diff. SLOPES	98.943	5.881	0.041	12	73.690
S (DIST + L _F), linear, diff. INTS comm. SLOPE	100.647	7.585	0.017	11	77.591

Note: Models estimate survival (S) and also incorporate fork length (L_F) as an individual covariate and release site (REL) as a batch-level covariate. The shape of the assumed covariate-survival relationship is stated (either linear or quadratic) where applicable. Parameters were assumed to vary with distance from release (DIST, i.e. habitat-specific) or be consistent across all habitats (CON). Models are ranked based on Akaike Information Criterion adjusted for small sample size (AICc). Only those models with an AICc weight greater than 0.01 are shown.

Table B.4 – Pool of tested known-fate models for West River, Sheet Harbor, salmon smolt survival in 2008.

Model	AICc	Delta AICc	AICc weight	Number of Parameters	Deviance
S (CON)	71.631	0	0.185	1	69.586
S (DIST + L _F), linear, diff. INTS comm. SLOPE	71.678	0.047	0.181	8	53.922
S (DIST)	71.732	0.101	0.176	7	56.383
S (L _F), linear	72.051	0.420	0.150	2	67.915
S (TWR), linear, comm. SLOPE comm. INT	72.280	0.649	0.134	2	68.143
S (L _F), quadratic	73.736	2.105	0.065	3	67.460
S (d * L _F), linear, comm. INT diff. SLOPES	74.021	2.390	0.056	8	56.265
S (d * TWR), linear, comm. INT diff. SLOPES	75.016	3.384	0.034	8	57.260

Note: Models estimate survival (S) and also incorporate fork length (L_F) or tag-to-body-weight ratio (TWR) as individual covariates. The shape of the assumed covariate-survival relationship is stated (either linear or quadratic) where applicable. Parameters were assumed to vary with distance from release (DIST, i.e. habitat-specific) or be consistent across all habitats (CON). Models are ranked based on Akaike Information Criterion adjusted for small sample size (AICc). Only those models with an AICc weight greater than 0.01 are shown.

Table B.5 – Pool of tested known-fate models for West River, Sheet Harbor, salmon smolt survival in 2009.

Model	AICc	Delta AICc	AICc weight	Number of Parameters	Deviance
S (DIST + L _F), linear, diff. INTS comm. SLOPE	61.238	0	0.349	7	46.246
S (DIST)	61.257	0.020	0.346	6	48.520
S (DIST+ TWR), linear, diff. INTS comm. SLOPE	62.883	1.646	0.153	7	47.892
S (DIST * TWR), linear, comm. INT diff. SLOPES	64.445	3.208	0.070	7	49.454
S (DIST * TWR), linear, diff. INTS diff. SLOPES	64.895	3.657	0.056	12	38.006

Note: Models estimate survival (S) and also incorporate fork length (L_F) or tag-to-body-weight ratio (TWR) as individual covariates. The shape of the assumed covariate-survival relationship is stated (either linear or quadratic) where applicable. Parameters were assumed to vary with distance from release (DIST, i.e. habitat-specific) or be consistent across all habitats (CON). Models are ranked based on Akaike Information Criterion adjusted for small sample size (AICc). Only those models with an AICc weight greater than 0.01 are shown.

Table B.6 – Pool of tested known-fate models for West River, Sheet Harbor, salmon smolt survival in 2010.

Model	AICc	Delta AICc	AICc weight	Number of Parameters	Deviance
S (CON)	108.466	0	0.429	1	106.444
S (L _F), quadratic	110.201	1.735	0.180	3	104.066
S (L _F), linear	110.313	1.847	0.170	2	106.246
S (TWR), linear	110.465	2.000	0.158	2	106.398
S (DIST), linear	113.404	4.938	0.036	9	94.358
S (DIST + L _F), linear, diff. INT comm. SLOPE	115.434	6.968	0.013	10	94.147
S (DIST + TWR), linear, diff.INT comm. SLOPE	115.597	7.131	0.012	10	94.310

Note: Models estimate survival (S) and also incorporate fork length (L_F) or tag-to-body-weight ratio (TWR) as individual covariates. The shape of the assumed covariate-survival relationship is stated (either linear or quadratic) where applicable. Parameters were assumed to vary with distance from release (DIST, i.e. habitat-specific) or be consistent across all habitats (CON). Models are ranked based on Akaike Information Criterion adjusted for small sample size (AICc). Only those models with an AICc weight greater than 0.01 are shown.

APPENDIX C: CORMACK-JOLLY-SEBER MODEL POOLS FOR CHAPTER 5

Table C.1- Pool of Cormack-Jolly-Seber models for salmon smolts from the Stewiacke River 2008, 2011 and Gaspereau River 2011.

Model	QAICc	Delta QAICc	QAICc Weights	No. Par.	QDeviance
<i>Gaspereau 2011</i>					
S (DIST) p (CON)	96.580	0.000	0.883	3	28.130
S (CON) p (CON)	100.703	4.123	0.112	2	34.441
S (CON) p (DIST)	107.429	10.849	0.004	8	26.948
S (DIST) p (DIST)	111.602	15.021	0.000	13	16.903
<i>Stewiacke 2008</i>					
S (DIST) p (DIST)	150.860	0.000	0.995	11	41.392
S (DIST) p (CON)	161.780	10.920	0.004	7	61.489
S (CON) p (CON)	166.740	15.880	0.000	2	77.187
S (CON) p (DIST)	170.207	19.347	0.000	7	69.915
S (GROUP) p (CON)	170.214	19.354	0.000	5	74.311
S (GROUP * DIST) p (CON)	196.943	46.083	0.000	25	50.458
S (GROUP * DIST) p (DIST)	211.348	60.488	0.000	29	52.617
S (GROUP) p (DIST)	856.943	706.083	0.000	10	749.821
<i>Stewiacke 2011</i>					
S (DIST) p (CON)	121.352	0.000	0.777	11	35.901
S (CON) p (DIST)	125.024	3.672	0.124	11	39.573
S (GROUP) p (DIST)	125.957	4.605	0.078	12	38.112
S (DIST) p (DIST)	129.019	7.668	0.017	19	23.298
S (CON) p (CON)	132.874	11.522	0.002	2	67.398
S (GROUP) p (CON)	134.127	12.776	0.001	3	66.563
S (GROUP * DIST) p (CON)	135.282	13.930	0.001	21	24.063
S (GROUP * DIST) p (DIST)	147.401	26.049	0.000	29	12.195

Note: Models estimate survival (S) and encounter probability (p, i.e. detection efficiency). Parameters were modelled using explanatory variables of; distance from

head-of-tide (DIST) or a constant effect (CON, i.e. a single parameter for all distances), a release group effect (GROUP) and their interactions. Models are ranked based on second-order, quasi-likelihood Akaike Information Criterion (QAICc).

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