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ARTICLE

Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland, Nova Scotia, Canada

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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 mass 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.

Résumé : La télémétrie acoustique est un outil utile pour la surveillance de la survie et du comportement en estuaire des post-saumoneaux de saumon atlantique. Dans la plupart des cas, le taux de survie signalé est la fraction statique de post-saumoneaux marqués détectés et, si le moment et le lieu de la mortalité peuvent être mentionnés, les covariables du taux de survie ou de la relation entre le comportement migratoire et la survie sont moins souvent rapportées. Dans cette l'étude, nous avons fait appel à la télémétrie acoustique pour suivre des saumoneaux de saumon atlantique en migration de la mer vers quatre rivières de la Nouvelle-Écosse (Canada). Nous avons en outre vérifié le lien entre le comportement migratoire et le taux de survie et utilisé des modèles de marquage–recapture pour examiner la longueur du corps et le rapport entre le poids de la marque et celui du corps comme covariables éventuelles du taux de survie. Les impacts sur ce dernier étaient les plus forts dans les habitats estuariens situés les plus près de la limite de marée. Dans quatre sites, la longueur du corps avait une incidence sur le taux de survie. La forme et la variabilité spatiale de la relation entre la longueur du corps et le taux de survie ont mis en lumière des vecteurs de mortalité, faisant ressortir un rôle possible de la prédation et du stress osmotique. Si les déplacements migratoires répétés vers la terre ou vers la mer n'avaient pas d'incidence sur le taux de survie, une corrélation significative a cependant été notée entre le temps de résidence et le taux de survie. [Traduit par la Rédaction]

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, 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., Hvidsten 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) that may ultimately influence survival.

Predation in estuaries is likely high. Constricted spaces, such as estuaries, concentrate predators and likely increase predator–

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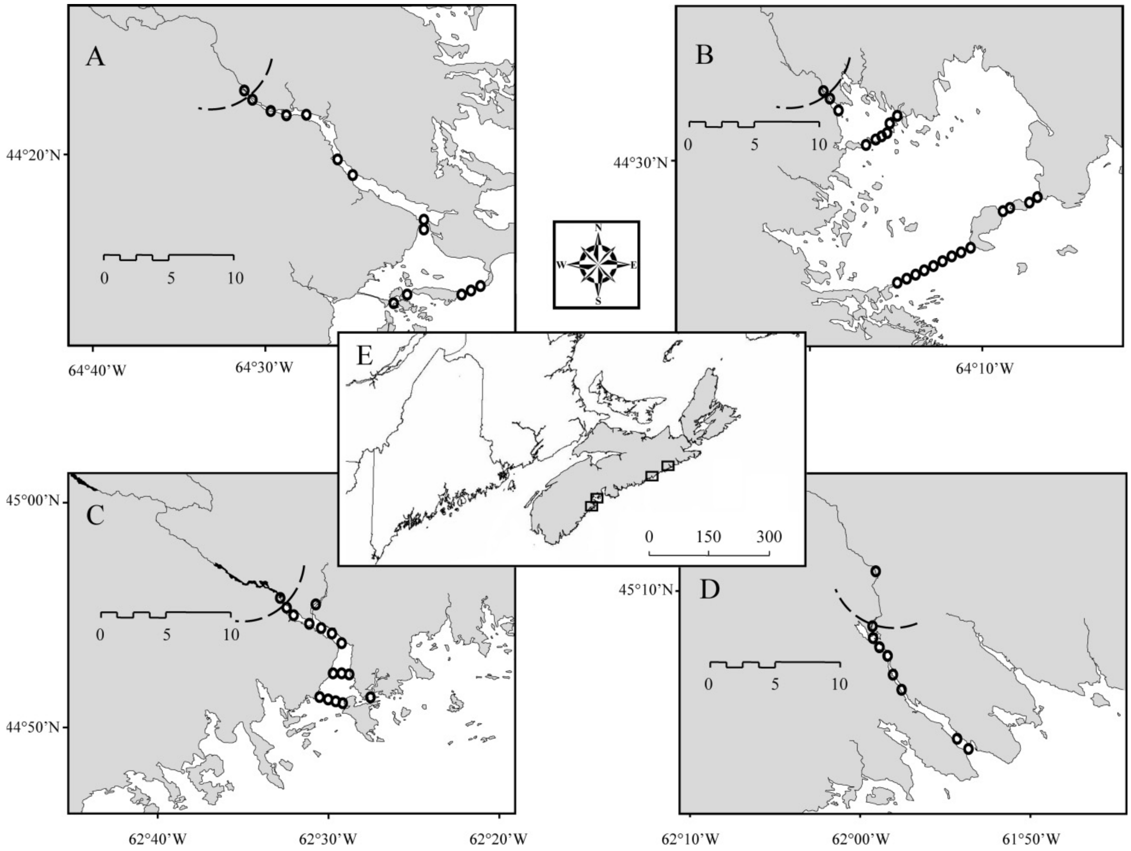
Fig. 1. Maps of the following study areas, from southwest to northeast: (A) Lahave River; (B) Gold River; (C) West River, Sheet Harbour; (D) St Mary's River; and (E) their relative locations (black boxes) within Nova Scotia. The location of all 2010 receivers (open circles) and approximate location of 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).



prey encounters (Brown and Mate 1983; Blackwell and Juanes 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 is 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.

Materials and methods

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. 1). These rivers lie in the Southern Upland, a geological region severely affected by anthropogenic acidification (Watt et al. 1983, 2000). Year of tagging and sample size for each of the four study rivers in order of increasing mean ambient river pH were as follows: 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; 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. 1). Receivers were mounted approximately 1–3 m above bottom. Active tracking was also periodically conducted, where a mobile receiver was soaked for >120 s at predetermined GPS coordinates 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).

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 (*i*) a tagged smolt ceased movement over an extended period of time, (*ii*) a tagged smolt was not detected leaving the study area by the end of the study, or (*iii*) 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 (*i*) survive to reach the receiver and (*ii*) be detected by the receiver. As such, both survival and detection efficiency 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 <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 1998). Second, in river-years where detection efficiency was 100% at all receiver locations (West River 2008, 2009, 2010, and St. Mary's River 2010), 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 they 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 mass ratio (TMR) were included as covariates after being z-transformed to increase comparability among populations where covariates significantly differed (e.g., L_F). TMR was included as a method of accounting for potential tag-burden effects, although it is somewhat confounded with L_F, as body mass is positively correlated with L_F, and thus longer smolts had a lower TMR. We ignored potential growth during the study and assumed that L_F and mass 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.

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 (*i*) reversal behaviour and (*ii*) 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 data set, 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 per km) 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 Tukey's 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. Goodness-of-fit was assessed for all final GLMs following the decile method of Hosmer and Lemeshow (1980) and Hosmer et al. (1991).

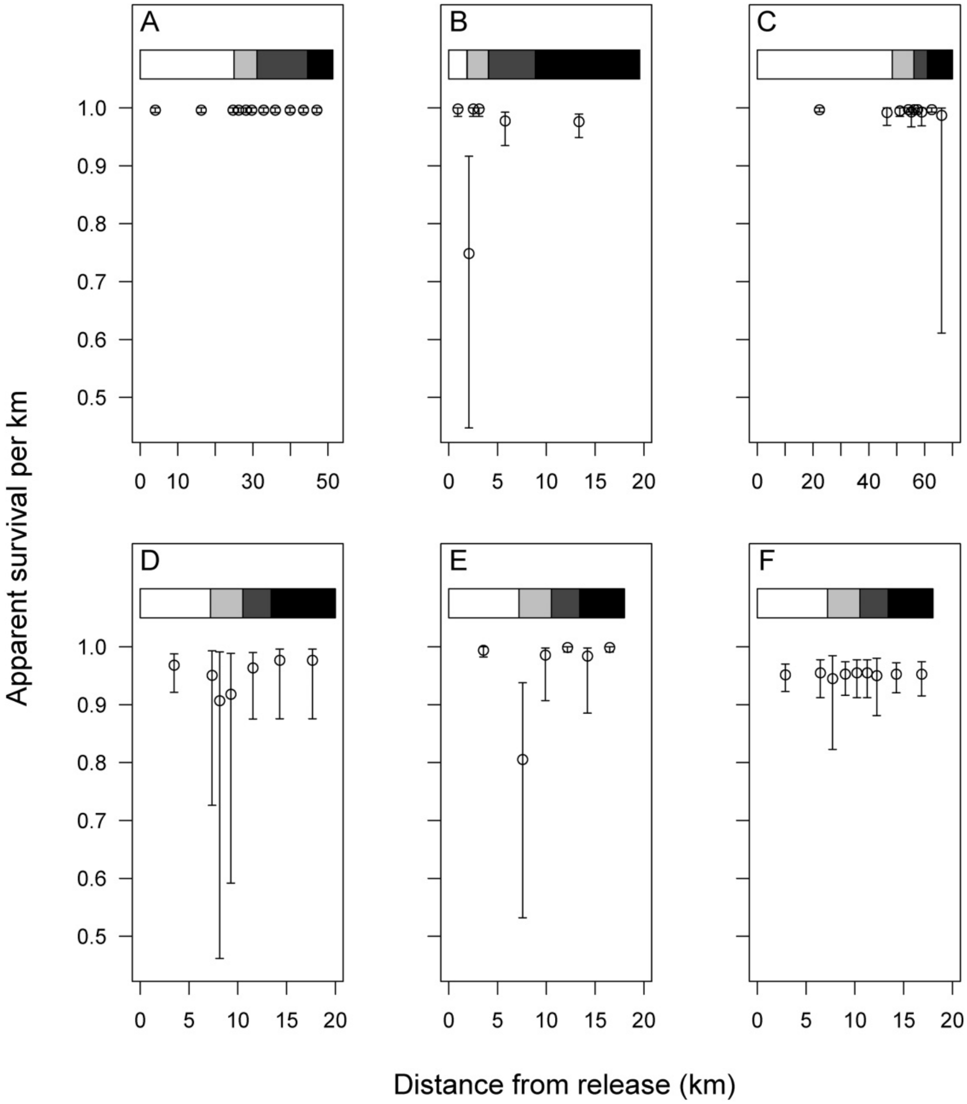
Results

Using 10 moored range-testing tags, we were able to validate our assumptions regarding detection ranges and estimate detection efficiencies 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. During any given active tracking "search", the likelihood of detecting a tagged postsmolt (if present) was 88% ± 19% (mean ± SD) in inner and outer estuary habitats, however, efficiency dropped to 58% ± 30% (mean ± SD) in bay habitats. In any given river-year, the probability of detecting a tagged postsmolt at least once during active tracking (if present) was approximately 95%.

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 data sets (Gold River, West River 2008, 2009, and 2010). There was insufficient support for habitat-specific survival in the

Fig. 2. Estimates (95% CI) of apparent survival for each river-year, at each receiver interval, as a function of distance from release in (A) the Lahave River, (B) Gold River, (C) St. Mary's River, (D) West River 2008, (E) 2009, and (F) 2010. Estimates were derived from a model averaging the pool of Cormack–Jolly–Seber models (Lahave and Gold) and known-fate models (St. Mary's, West 2008, 2009, 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.



remaining two data sets (Fig. 2; supplementary Tables S1–S6[1]), which were best described by constant rates of survival (Fig. 2; Tables S5 and S6). 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 TMR which is roughly inversely proportional to L_F) as a covariate significantly improved the explanatory power of the models for all data sets except the St. Mary's River (Tables S1–S6). Covariates did not influence survival consistently among data sets (Fig. 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.

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 and 13.9 days (mean = 3.9, SD = 4.3) after entering the estuary (Fig. 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). We used the mean estimates of the probability that a smolt would have performed

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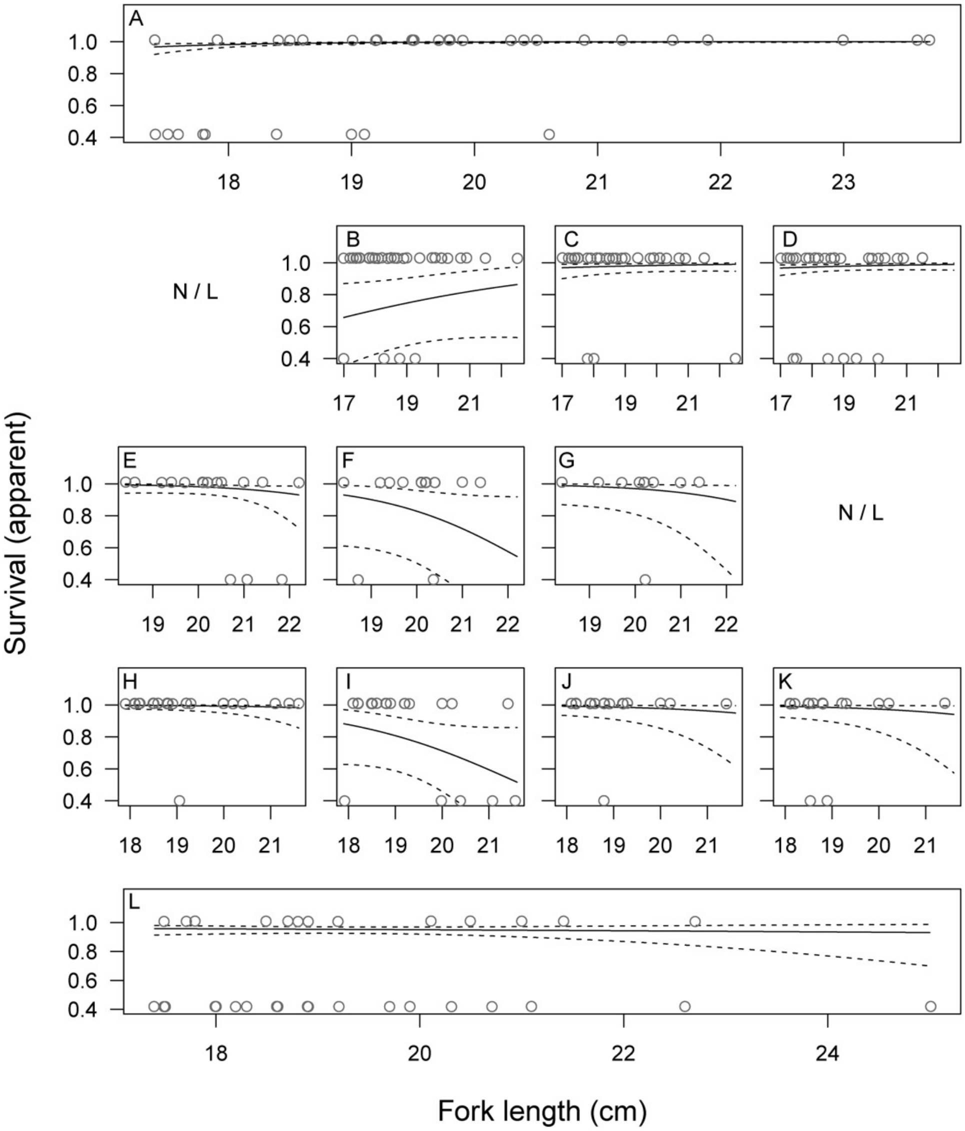
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0287.

Fig. 3. Plots of covariate (fork length; cm) effects on apparent survival per kilometre. 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: (A) Lahave River, all habitats zones; (B) Gold River, inner estuary; (C) Gold River, outer estuary; (D) Gold River, bay; (E) West River 2008, freshwater; (F) West River 2008, inner estuary; (G) West River 2008, outer estuary; (H) West River 2009, freshwater; (I) West River 2009, inner estuary; (J) West River 2009, outer estuary; (K) West River 2009, bay; and (L) West River 2010, all habitats zones. 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.



reversals, if it had not died, to calculate the true proportion of postsmolts performing reversals. In this analysis we found insufficient support (*G* test: df = 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: df = 1, p = 0.047).

Standardized overall residency was a significant predictor of survival for smolts from the Gold River and West River 2010 model and from the West River 2008 and 2009 model, but not for smolts from the Lahave and St. Mary's rivers model (Table 1). The model for Gold River and West River 2010 appeared to fit the data adequately; however, there was evidence of significant lack of fit for the West River 2008 and 2009 model (Table 2). There was support for inclusion of a quadratic residency term in the model for Gold River and West River 2010 (Table 1), where survival was predicted to increase with increasing residency between values of approximately 0–2 days·km^{-1}, decreasing thereafter (Fig. 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

Fig. 4. (A) Cumulative incidence (cumulative probability) curves of likelihood of performing a migration reversal (solid line) and likelihood of mortality without reversals (dashed 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.

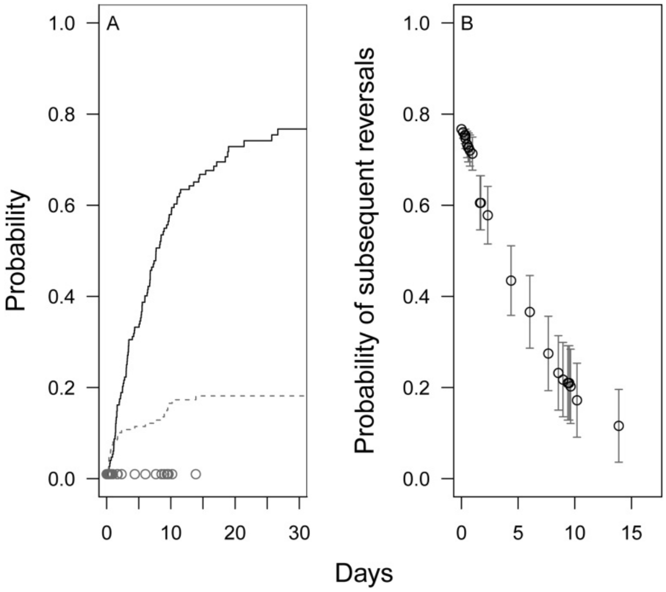


Table 1. Logits of parameter (β) and standard error (SE) estimates for generalized linear models with binomial error distributions.

Models and terms	β estimate	SE	z	Pr > z
Lahave and St. Mary's				
SOR	–1.490	1.241	–1.201	0.230
Gold and West 2010				
SOR	6.100	1.924	3.171	0.002
SOR²	–1.618	0.495	–3.273	0.001
West 2008 and 2009				
SOR	4.003	1.258	3.181	0.001

Note: Dependant data were binary fate (0 = died, 1 = survived) and the explanatory variable was of standardized overall residency (SOR) or the square of SOR.

salmon. The examination of survival correlates may add additional value to telemetry studies and provide important insight to potential mechanisms underlying observations of mortality.

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 >0.90·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 showed significant losses over short spatial scales (particularly for the inner estuaries of Gold and West rivers); however, mortality rates through the remainder of habitats and estuaries that this study monitored were not particularly high relative to the estimated subsequent mortalities that salmon from the study rivers are believed to have been experiencing (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 mass was held constant in this study, and thus TMR 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 TMR 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.

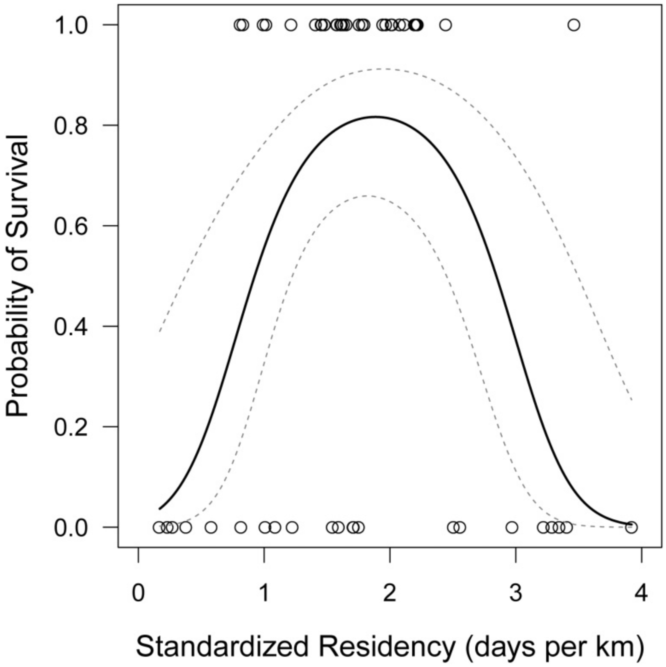
Spatial trends of the impact of covariates and their strength, both habitat-specific and among river, may also provide insight toward mortality vectors. Among-habitat variability in the shape of the L_F–survival relationship highlights those habitats where selective pressures are most intense. In our data sets, 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 salt water 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.

Table 2. Diagnostic results of generalized linear models, with binomial error distributions, for each of the three river-year groupings.

						Goodness-of-fit		
River-Year	Model terms	Null deviance	Residual deviance	Deviance explained (%)	Residual df (null df)	$\hat{c}$	df	p
Lahave and St. Mary's	Fate ~ SOR	49.72	48.30	2.86	55 (56)	17.48	8	0.025
Gold and West 2010	Fate ~ SOR + SOR²	75.04	56.06	25.29	53 (55)	11.91	8	0.155
West 2008 and 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 per km), and the square of SOR. Goodness-of-fit was calculated using the Hosmer–Lemeshow decile test (Hosmer and Lemeshow 1980; Hosmer et al. 1991). Goodness-of-fit p values < 0.05 indicate a significant lack of fit.

Fig. 5. The relationship between standardized (days per km) 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 line is the predicted logistic regression and dashed lines are the 95% confidence bands.



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.

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 influences 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 nonsignificant 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. Watt et al. (2000) classified the Gold and West rivers as the most acidic in the region, with a mean pH between 4.7 and 5.4, which is likely to cause significant mortality of salmon in fresh water (Lacroix 1989; Farmer 2000) and also reduce marine survival (Staurnes et al. 1996; Kroglund et al. 2007). By contrast, the Lahave and St. Mary's rivers have a mean pH > 5.4, which is not expected to significantly impact survival (Lacroix 1989; Farmer 2000). Although this study was not designed to test effect of river pH on subsequent postsmolt survival, the different relationships between survival and residency in rivers that differ in pH warrants further study. 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 reduces 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 facilitating the transition from fresh water to salt water by decreasing osmoregulatory stress. However, the negative second quadratic term shown in Fig. 5 likely describes an alternative mechanism, most probably predation-related mortality. Because predation pressure in estuaries is frequently high (this study; see also Hvidsten and Møkkelgjerd 1987; Dieperink et al., 2002; Jepsen et al. 2006), a negative relationship may reflect the effect of increased exposure to predation. Therefore, we interpret the overall humped trend as a trade-off related to optimization, where postsmolts stay in the estuary long enough to adjust to saline water, but not so long as to suffer excess predation mortality.

Reversal behaviour may also reflect a behavioural response of animals damaged by acidic water to increasing salinity and the associated osmotic stress (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. This seems counterintuitive given the considerable literature suggesting that survival is influenced by acid-induced stress (e.g., Staurnes et al. 1996; Kroglund and Finstad 2003; Kroglund et al. 2007) and the fact that the animals in this study from highly acidified sites showed increased estuarine residency. Previous studies reporting reversal behaviour have been from both acidified rivers (Magee et al. 2001; Kocik et al. 2009; Halfyard et al. 2012) and nonacidified rivers (Martin et al. 2009; Dempson et al. 2011), and thus the animals may reverse their movements for multiple reasons including acclimation to temperature gradients (Dempson et al. 2011). At this time we cannot provide a definitive explanation for why our fish reversed direction.

Our results support the theory that mortality of Atlantic salmon postsmolts in estuaries is high across short distances, 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 will be important for understanding behavioural differences among smolts and the implication for future conservation planning.

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