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ARTICLE

Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts

A. Jamie F. Gibson, Edmund A. Halfyard, Rod G. Bradford, Michael J.W. Stokesbury, and Anna M. Redden

Abstract: Telemetry is increasingly being used to estimate population-level survival rates. However, these estimates may be affected by the detectability of telemetry tags and are reliant on the assumption that telemetry data represent the movements of the tagged fish. Predation on tagged fish has the potential to bias survival estimates, and unlike the issue of detectability, methods to correct for the resulting bias (termed "predation bias") are not yet developed. In an acoustic telemetry study on inner Bay of Fundy Atlantic salmon (*Salmo salar*) smolts during 2008 and 2011, unusual tag detection patterns were indicative that some data may have been representative of the movements of predators rather than smolts. To incorporate predation effects into the resulting survival estimates, a suite of 11 summary migration metrics were compared between Atlantic salmon smolts and striped bass (*Morone saxatilis*). Cluster analyses revealed that 2.4% to 13.6% of tags implanted in smolts exhibited migration patterns more similar to striped bass than to other smolts, which was interpreted here as evidence of predation. Reassigning the fate of these tags as "depredated–died" reduced estimated survival from 43.5% to 41.1% in 2008 and from 32.6% to 19.0% in 2011 relative to a traditional mark–recapture model, illustrating the effect of predation bias in this case study.

Résumé : L'utilisation de la télémétrie pour estimer les taux de survie à l'échelle de la population est de plus en plus répandue. Ces estimations peuvent toutefois être influencées par la détectabilité des étiquettes utilisées et reposent sur le principe que les données de télémétrie rendent compte des déplacements des poissons marqués. La prédation de ces derniers pourrait cependant biaiser les estimations des taux de survie et, contrairement au problème de détectabilité, il n'existe pas encore de méthode permettant de corriger le biais qui en résulte (appelé « biais de prédation »). Dans une étude de télémétrie acoustique portant sur des saumoneaux de saumon atlantique (*Salmo salar*) de la haute baie de Fundy, menée en 2008 et 2011, des motifs de détection d'étiquettes inhabituels indiquaient que certaines données pouvaient refléter les déplacements de prédateurs plutôt que ceux des saumoneaux. Afin d'intégrer les effets de la prédation dans les estimations des taux de survie en découlant, 11 paramètres sommaires associés à la migration de saumoneaux de saumon atlantique et de bars d'Amérique (*Morone saxatilis*) ont été comparés. Des analyses typologiques ont révélé que de 2,4 % à 13,6 % des étiquettes implantées dans des saumoneaux témoignaient d'habitudes migratoires plus semblables à celles de bars d'Amérique qu'à celles d'autres saumoneaux, ce qui a été interprété comme une preuve de prédation. La réaffectation du destin de ces étiquettes à des individus « morts–victimes de prédation » s'est traduite par une réduction des taux de survie estimés de 43,5 % à 41,1 % pour 2008, et de 32,6 % à 19,0 % pour 2011, par rapport aux résultats d'un modèle de marquage–recapture traditionnel, illustrant ainsi l'effet du biais de prédation dans cette étude de cas. [Traduit par la Rédaction]

Introduction

Quantifying the rate and timing of mortality is important for the 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. Although methods for estimating mortality rates have been developed based on traditional mark–recapture studies (e.g., Seber and Le Cren 1967; Pollock et al. 1991; Pine et al. 2003), recent advances in telemetry technologies that permit remote sensing of animal movement and behaviour are now providing new methods for estimating age- and stage-specific mortality rates, particularly on short temporal scales. In particular, acoustic telemetry has facilitated the estimation of survival for freshwater and marine fish populations (e.g., Heupel and Simpfendorfer 2002; Hubley et al. 2008; Stokesbury et al. 2011).

Survival estimates using acoustic telemetry data are dependent on several critical assumptions, two of which are (*i*) tagged fish have some probability of being detected when in proximity to a receiver, and (*ii*) 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 used for 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. A scenario that would violate this second assumption occurs if a tagged fish is consumed by a predator or scavenger, and the subsequent movement of the predator–scavenger is then monitored while the active tag continues to transmit signals from within the gastrointestinal tract of the predator. If the tagged fish is assumed to be alive because of the movement of the tag, survival estimates will be biased high, a phenomenon referred to here as "predation bias".

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A.J.F. Gibson and R.G. Bradford. Fisheries and Oceans Canada, 1 Challenger Drive, Dartmouth, NS B2Y 4A2, Canada.
E.A. Halfyard. Fisheries and Oceans Canada, 1 Challenger Drive, Dartmouth, NS B2Y 4A2, Canada; Biology Department, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada.
M.J.W. Stokesbury and A.M. Redden. Biology Department, Acadia University, 33 Westwood Avenue, Wolfville, NS B3P 2R6, Canada.
Corresponding author: A. Jamie F. Gibson (e-mail: jamie.gibson@dfo-mpo.gc.ca).

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Methods to identify predation–scavenging events in acoustic telemetry studies, and to correct for predation bias, are not well developed.

Based on assumed differences in the behaviour of prey and predators, tag movement characteristics have been used to infer predation events. For example, the apparent reversal of migratory behaviour of Atlantic salmon (*Salmo salar*) smolts (i.e., alternating upstream and downstream movements) was interpreted by Beland et al. (2001) as potential predation by striped bass (*Morone saxatilis*). Tag movement patterns have also been used to infer mortality in other species, such as assuming that stationary tags represent dead individuals (e.g.,Yergey et al. 2012), assuming that signals lost from study sites represent avian predation (e.g., Halfyard et al. 2012), or assuming that abnormal behaviour represented predation (e.g., Morrissey and Gruber 1993; Heupel and Simpfendorfer 2002; Melnychuk et al. 2013). Ancillary sensor data, such as depth or temperature, can also provide evidence of predation events (e.g., Thorstad et al. 2011*a*); however, acoustic tags outfitted with sensors are larger than acoustic tags without sensors and therefore may not be suitable for many small fishes. Ancillary sensor data from other telemetry technologies have been used to infer predation events (e.g., Béguer-Pon et al. 2012; Lacroix 2014; Wahlberg et al. 2014), 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.

In this paper, we provide a simple model for the number of tags detected during acoustic telemetry studies that illustrates how predation bias can affect survival estimates. As shown in the model, an estimate of the number of tags consumed and being carried within predators is required to quantify predation effects, a parameter that is typically unknown. For our case study, we developed a method based on a cluster analysis of migration behavior metrics of both our target species and one of its predators to identify fish that may have been consumed by a predator. After quantifying predation events, we are able to contrast the survival estimates from acoustic telemetry data obtained using a mark–recapture model that incorporates tag detection efficiency with a similar model that also incorporates predation effects.

We illustrate the approach using a study undertaken to estimate the estuarine survival of Atlantic salmon smolts from two inner Bay of Fundy (iBoF) Atlantic salmon populations. Detailed information about the timing and magnitude of mortality is critical for the development of conservation and recovery plans for the endangered Atlantic salmon population assemblages in eastern North America, and there is public concern over the potential effect of striped bass predation on the success of 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 Juanes 1998; Beland et al. 2001; Kocik et al. 2009) and also by divergent trends in the populations of salmon (decreasing) and striped bass (increasing) within the Gulf of Maine and Bay of Fundy. We used data from a concurrent telemetry study for striped bass (Bradford et al., in press) to compare the movements of tags placed in salmon smolts with those placed in striped bass to investigate if predation events could be identified using a cluster analysis of movement metrics. We then used the results from these analyses to adjust the survival estimates for smolts for predation bias. Although the cluster-based analyses likely do not fully account for predation effects, the analyses do provide a basis for discussing the impact of failure to address predation when estimating survival from telemetry data as well as the implications of the study for recovery planning for iBoF salmon.

Methods

Predation bias in survival estimates from telemetry studies

Consider a system in which animals are tagged at the onset of migration and their subsequent survival is estimated via remote tag detection as animals move along a migration corridor in which predators are present. Because the animals are not observed directly, the movement of the tag may be indicative of the movement of the tagged animal or the movement of a predator that has consumed the tag. Acoustic tracking of salmon smolts migrating downstream through rivers and estuaries is an example of such a system. Assuming that the detection efficiency is the same for tags being carried by live smolts and tags in the stomach of a predator, in the deterministic case, a simple model for the number of tags detected at some point during migration, N_{detected}, is

$$N_{\text{detected}} = (N_{\text{released}} - N_{\text{died}} + N_{\text{in-predator}})d \tag{1}$$

where N_{released} is the number of tagged animals released at the start of the study, N_{died} is the total number of animals that died from all causes between the point of release to the point of detection, $N_{\text{in-predator}}$ is the number of tags being carried within the gut of a predator that are subsequently detected, and d is probability that tags are detected at the point of detection. Tags being carried by a predator are a component of those that died. Dividing both sides first by d, and then by N_{released}, and using P for the resulting proportions, yields

$$\frac{P_{\text{detected}}}{d} = 1 - P_{\text{died}} + P_{\text{in-predator}} \tag{2}$$

The term on the left-hand side of the equation is the equivalent of the detection-efficiency-adjusted survival rate estimates reported, for example, in some Atlantic salmon smolt telemetry studies (e.g., Davidsen et al. 2009; Kocik et al. 2009; Halfyard et al. 2013), denoted here as S_d. The term $(1 - P_{\text{died}})$ is the actual survival (S) that is typically the quantity of interest in these types of studies. The term $P_{\text{in-predator}}$ is an unknown quantity. Rearranging the equation yields

$$S = S_d - P_{\text{in-predator}} \tag{3}$$

which shows that if some tag detections in the study are actually indicative of the movement of predators, then the resulting survival estimates are biased by an amount equal to the proportion of the released tags that are detected in predators (note that if the detection efficiency differs between tags in predators and in live smolts, the magnitude of the bias will also differ). To adjust for this bias, the number of tags that have been consumed needs to be estimated, which is typically not known. In our case study with iBoF Atlantic salmon, this was accomplished using a cluster analysis of the movement metrics of both the study species and one of its main predators, as described later in this manuscript.

Study populations

Inner Bay of Fundy Atlantic salmon are currently listed as "Endangered" under the Canada's Species at Risk Act. There are 42 rivers and streams within the iBoF region thought to have supported Atlantic salmon populations in the past (DFO 2008), and there is evidence that many populations are now extirpated (Gibson et al. 2004). Abundance of adult salmon returning to iBoF rivers was estimated to have been 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). Survival during the estuarine and marine phase of their life cycle currently limits population growth and has been responsible for the major declines

Table 1. Summary of the acoustic tagging of Atlantic salmon smolts and river and estuary receiver deployments in the Gaspereau and Stewiacke rivers in 2008 and 2011.

River	Year	Release	Release date	No. released	Tag model	Mean (SD) fork length (mm)	No. of receivers
Gaspereau	2011	2	17 May	20	V9-6 L	193 (8)	7
Stewiacke	2011	1	25 May	12	V9-6 L	147 (6)	8
Stewiacke	2011	2	27 May	15	V9-6 L	150 (8)	8
Stewiacke	2008	1	23 May	19	V9-6 L	NA	6
Stewiacke	2008	2	30 May	22	V9-6 L	NA	6
Stewiacke	2008	3	6 June	15	V9-6 L	168 (11)	6
Stewiacke	2008	4	13 June	10	V9-6 L	164 (8)	6

that have placed this group of 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).

The migration of salmon smolts from two iBoF Atlantic salmon populations was monitored during this study. These populations, which inhabit the Stewiacke River and the Gaspereau River, have different life history characteristics. Stewiacke River salmon mature predominantly after one winter at sea with a comparatively higher frequency of repeat spawning (Chaput et al. 2006). Based on returns of Carlin tags from 1970 to 1990, they 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 matures after two winters at sea with a lower frequency of repeat spawning (Chaput et al. 2006). Based on tag returns from a similar time period, at least a portion of the population migrates to the waters off West Greenland (Amiro 2003).

Field methods, tagging, and telemetry

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 approximately 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, Oregon, 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 methanesulphonate (MS-222, Syndell Laboratories, Vancouver, British Columbia, Canada), until reaching stage 4 anaesthesia, which, dependent in part on water temperature, was generally in the range of 180 to 240 s. 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, 2.9 g in air, 9 mm by 24 mm, Amirix/Vemco, Bedford, Nova Scotia., Canada) were implanted in the intraperitoneal cavity via a single incision (approximately 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. Postsurgery smolts were allowed to recover from the effects of anesthesia (approximately 24 h), 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 mass to smolt mass averaged 7.0% (range: 4.9%–9.7%) in the Stewiacke River in 2008, 10.0% (range: 8.0%–14.4%) in the Stewiacke River in 2011, and 4.3% (range: 3.2%–5.3%) in the Gaspereau River in 2011. Tag size is a concern for all telemetry studies, and some tagging effect is likely to occur at all tag-to-body sizes (Perry et al. 2013); however, there is also a growing body of literature that some species of fish do not exhibit major mortality, tag loss, or sublethal impacts when tagged with devices that approach as much as 8%–12% of body mass (Cooke et al. 2011). Acoustic receivers (Vemco VR2 and VR2W) for tag detection 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 line 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, Nova Scotia (Hebert et al. 2009), provided ancillary detections in the Minas Basin and the North Atlantic Ocean that were used to improve efficiency estimates for the receivers in the rivers and estuaries.

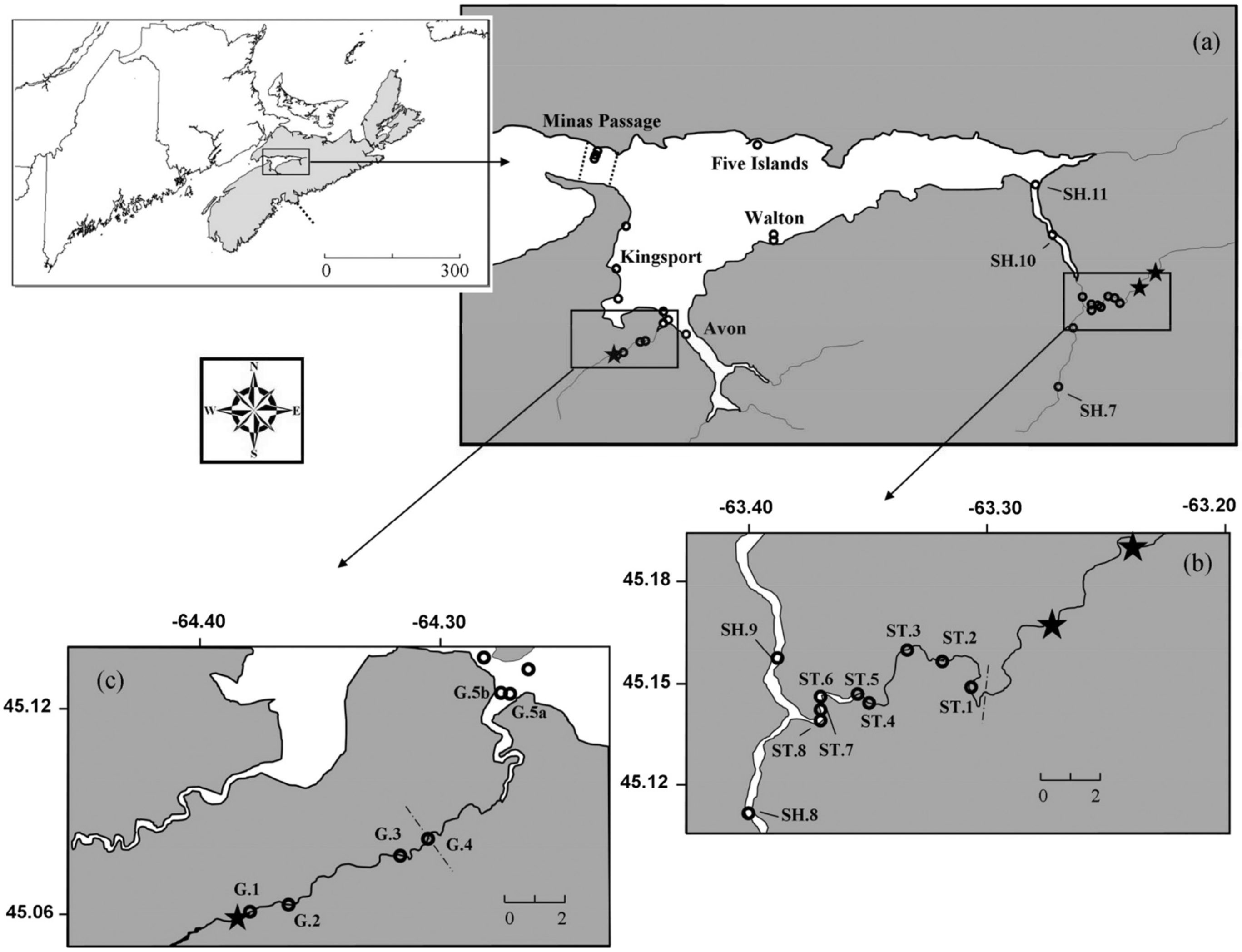
The tagging procedure can induce additional handling stress on smolts that may lead to tagging-induced mortality (e.g., Lacroix et al. 2004; Brown et al. 2010; Sandstrom et al. 2013), which should be considered when estimating mortality rates. To reduce the effects of handling-induced mortality, in addition to holding salmon for 24 h after tagging and prior to release, we estimated survival using only those smolts that were detected on any downstream receiver. In the Gaspereau River, smolts not detected by one of the two most upstream receivers (maximum 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 were not detected by these receivers after release.

Analytical methods

All acoustic telemetry data were compiled in Vemco VUE software, mark–recapture modelling was conducted using the program MARK (White and Burnham 1999), and subsequent analyses were conducted in R 3.0.2 (R Core Team; www.r-project.org). Initial analyses of the telemetry data led to the identification of several tags that exhibited behaviours that we considered atypical for Atlantic salmon smolts based on current knowledge of salmon behaviour in estuaries (e.g., exhibiting many migration reversals in the estuaries, particularly in an area known to be spawning habitat for striped bass; migrating upstream in nearby estuaries). 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

Fig. 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 (circles), and release sites (stars). Also shown are the receiver arrays at Halifax and within the Minas Passage (dotted lines) and the head-of-tide (dashed lines) 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.



the effect of gear performance (i.e., detection probability) and the confounding effects of predation. To this end, we calculated and compared survival estimates using two methods, including (*i*) a Cormack–Jolly–Seber (CJS) mark–recapture modeling approach that accounts for detection probability and (*ii*) a CJS approach adjusted for predation bias, based on a cluster analysis of behavioural characteristics used to identify tags within the gut of a predator.

Analytical methods: CJS survival estimates

To account for receiver detection efficiencies less than 100% and differences in detection efficiency among receivers, we estimated survival using CJS mark–recapture models (Cormack 1964; Jolly 1965; Seber 1965), a technique that has been previously applied to Atlantic salmon telemetry data (e.g., Davidsen et al. 2009; 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, we can adapt CJS models from a time-based encounter history to a spatially based encounter history, where events take place at each receiver location and the sampling interval across which survival is estimated is the distance between receivers (Burnham et al. 1987). Reported survival estimates were standardized by the distance between receivers ($S\cdot\text{km}^{-1}$) to facilitate comparison.

A fully parameterized global model was set up for each of the three river–year combinations, where survivals and detection probabilities were estimated for each receiver (REC), each release group (GROUP), and their interactions. All models were fit using a logit link function. 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). Further, in an effort to flag poorly fit models, all were examined for evidence of parameter estimates approaching the bounds, unexpectedly large variance estimates, and failures to converge, although the latter is difficult to assess quantitatively.

Pools of nested models were derived from each of the three global models, and model comparison were made using quasi-likelihood Akaike information criterion (QAIC), where smaller values indicate a more parsimonious value. QAIC is similar to Akaike information criterion in that it addresses issues of balance between under- and over-fit models and formally weighs model bias and variance trade-offs (Burnham and Anderson 2004), but also adjusts values for lack of fit (i.e., overdispersion) in cases where $\hat{c}$ was greater than 1.0. 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 QAIC value (QAICc). In all cases, several models showed utility in describing the data (i.e., QAICc values were not very different). Therefore, to incorporate the information of all suitable models, final parameter estimates were derived via weighted (by QAICc values) model averaging (Johnson and Omland 2004).

Analytical methods: cluster analysis of Atlantic salmon and striped bass movement metrics

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., in press) as they exited their overwintering 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 (range: 410 to 898 mm). Data from 13 striped bass were included from the 2011 season with a mean total length of 654 mm (range: 545 to 780 mm).

Cluster analyses were used to identify structuring among the movement characteristics 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 calculated 11 (10 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*, total number of migration direction reversals; *j*, 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 detected within the time period when tagged smolts were detected in these estuaries: 23 May to 23 June (2008), and 25 May to 6 July (2011). Striped bass data were similarly confined to these time periods.

Empty matrix cells were assigned a zero, because missing cells represented actual differences in fish behaviour and not gear malfunctions (e.g., no upstream migration speed estimate owing to downstream-only migration). Data used in the matrix were both centred (column values – column mean) and scaled (column values – column standard deviation), as variables with larger scale (e.g., total number of detections, thousands) would contribute more to distance measures compared with those at a smaller scale (e.g., number of reversals, tens). Differences in movement variables among tags were analyzed from a symmetrical matrix of Euclidean distances (Legendre and Legendre 1998; Borcard et al. 2011).

A hierarchical clustering approach using Ward's minimum variance method (Ward 1963) was selected, and the analysis was implemented using the "hclust" function in the "base" package of R 3.0.2 (R 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. Ward's method then uses a centroid link to identify the mean distance of this new cluster and then compares it with 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 this sharp decline occurs is partially subjective; however, the between-tag structuring of the resultant cluster dendogram would remain the same regardless of number of clusters retained.

To test the magnitude by which certain migration parameters influenced the outcome of the cluster analyses, we conducted a sensitivity analysis in which varying combinations of input parameters were excluded from the analyses. In addition to the full model that included all parameters, six (2008) and four (2011) subsets of parameters were tested. Input parameters for each of the four trials consisted of all parameters except the following: the total time on spawning grounds (trial 1), the total number of reversals and total displacement (trial 2), the four speed metrics (trial 3), and the total number of detections and the total number of days with detections (trial 4). The additional two trials used in 2008 consisted of all parameters less the total detections in the Shubenacadie River above the confluence with Stewiacke River (trial 5) and 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 (trial 6).

Cluster analyses identified similarities in the movement characteristics among tags. We assumed that predation had occurred when smolt tags clustered with striped bass tags; however, interpreting these clusters was partially subjective and warranted (particularly in 2011) post hoc examination of differences in the mean migration metrics for each cluster. The cluster analyses identified individual smolt tags that were detected exiting the estuary but could be reassigned as having died (as a result of predation).

Analytical methods: predation-adjusted CJS survival estimates

The ratio of the number of tags that were detected exiting the estuary that were reassigned as having died (as a result of predation) to the number of smolts that were originally tagged and subsequently detected was used to calculate the predation bias adjustment. This adjustment was applied as per eq. 3. An identical adjustment can be obtained by multiplying the CJS survival estimate by the ratio of the number of tags that were not reassigned as having died to the number detected leaving the estuary.

Results

CJS-based survival estimates

A total of 78 salmon smolts were detected on the first receiver downstream from their respective release sites. In general, the proportion of tags detected decreased with distance from release, consistent with the cumulative nature of mortality (Table 2). In the Stewiacke River, the total number of detections at an individual receiver was highest in the area immediately downstream from the head-of-tide, while the distribution of absolute detections in the Gaspereau River was fairly homogeneous. In 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. In 2008, the proportion of tags detected at the mouth of the estuary was much higher for the two release events in May than for the two release events in June. In the Gaspereau River in 2011, eight unique tags were detected at the mouth of the estuary.

Table 2. Acoustic tag detection patterns for Atlantic salmon smolts tagged and released in the Gaspereau and Stewiacke rivers during 2008 and 2011, from the release location to the Minas Passage.

					No. detected at:				
River	Year	Release	No. released	No. with >1 total detections	Head-of-tide	Confluence of Stewiacke and Shubenacadie rivers	Mouth of estuary	Minas Basin	Minas Passage
Gaspereau	2011	2	20	15	14	NA	8	5 (0)[a]	7 (0)[a] (3)[b]
Stewiacke	2011	1	12	11	11	6	1	2 (1)[a]	1 (0)[a] (0)[b]
Stewiacke	2011	2	15	11	11	6	5	4 (1)[a]	1 (1)[a] (0)[b]
Stewiacke	2008	1	19	17	17	16	4	NA	NA
Stewiacke	2008	2	22	19	19	16	9	NA	NA
Stewiacke	2008	3	15	3	3	1	0	NA	NA
Stewiacke	2008	4	10	2	2	1	0	NA	NA

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.

[a] Number not detected at river mouth.

[b] Number not detected in the Minas Basin.

The deployment of receivers in the Minas Basin, Minas Passage, and offshore from Halifax in 2011 permitted additional detections that partially account for surviving salmon that reached the Minas Basin but were not detected at the river's mouth. 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 ($n = 2$) (Fig. 1). Three salmon from the Gaspereau River were detected at the Halifax receiver line.

Goodness-of-fit testing of the global CJS model in each dataset suggested that all models adequately fit the data, although there was some evidence of significant, albeit mild, lack of fit ($\hat{c} = 1.27$, $\hat{c} = 1.22$, and $\hat{c} = 1.07$ in in the Stewiacke River 2008, 2011 and Gaspereau River 2011, respectively). No other issues were identified with the model fits.

The Stewiacke River data from 2008 supported several models (Table 3). The most parsimonious model contained a group effect on survival with detection probability being receiver-specific. Survivals estimates (after model averaging) ranged from $90.4\%\cdot\text{km}^{-1}$ to $98.4\%\cdot\text{km}^{-1}$ (Fig. 2). Parameter estimates and their variance were poor for release groups 3 and 4 because of small sample sizes and sparse data. The overall cumulative survival estimate (of all release groups combined) to the mouth of the Shubenacadie estuary was 43.5%, spanning a distance of 35.7 km from the most upstream receiver.

In the Stewiacke River data from 2011, there was support for several models (Table 3).The most parsimonious model suggested that survival was constant, while detection probability was variable across receivers. Model-averaged survival estimates ranged from $90.6\%\cdot\text{km}^{-1}$ to $98.2\%\cdot\text{km}^{-1}$ (Fig. 2). Overall cumulative survival to the mouth of the Shubenacadie estuary was estimated to be 32.6%.

The Gaspereau River data from 2011 strongly supported a single model (QAICc weight >0.91, Table 3). This most parsimonious model suggested that survival was constant among receiver spacings and that detection probability was similar among receivers. Therefore, model-averaged survival estimates showed little variation, ranging from $96.8\%\cdot\text{km}^{-1}$ to $97.2\%\cdot\text{km}^{-1}$ (Fig. 2) and resulted in an overall cumulative survival to the mouth of the Gaspereau estuary of 57.3% across distance of 18.3 km from the most upstream receiver.

All CJS models account for tagging-induced mortalities by removing all individuals that failed to be detected by any receiver after release; thus, the estimated survival in the first interval (i.e., receiver spacing) was manually fixed at 100.0% to reflect this censoring.

Predation-adjusted survival rates based on the cluster analyses

The cluster analyses 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*a*), one containing exclusively striped bass (cluster 3, Fig. 3*a*), and one containing predominantly striped bass with three salmon smolts (cluster 2, Fig. 3*a*). A qualitative 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). In particular, the movement characteristics of individual tags belonging to cluster 1 were characterized by fewer total detections, few days with detections, few migration reversals, and lower total displacement, total time lapse, time on the striped bass spawning grounds, and migration speeds (Table 4).

The sensitivity analyses indicated that the clustering of Stewiacke 2008 data 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. Only one of the three salmon tags that clustered with the striped bass were initially classified as having exited the estuary (i.e., survived), as the other two were not detected at the mouth of the Shubenacadie estuary, but were detected on the second-last downstream receiver. Therefore, in 2008, the fate of one smolt was reassigned from having successfully exited the estuary to having died.

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 to each other than in the 2008 data (Fig. 3*b*). 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 that excluded the four speed-related parameters. One salmon tag and either one or two striped bass tags constantly grouped as outliers (cluster 1, Fig. 3*b*). These tags exhibited extreme values of all parameters, most typified by numerous reversals, extended time spent on the spawning grounds, and many tag detections (Table 5; Fig. 5). Second, a cluster of seven salmon tags (cluster 2, Fig. 3*b*) showed substantial segregation from the remaining tags in the full model and three of four sensitivity runs with subsets of data. Generally, these salmon exhibited unidirectional movements downstream as far

Table 3. Pool of Cormack–Jolly–Seber model results for survival and detection probability of acoustically tagged Atlantic salmon smolts from the Stewiacke River during 2008 and 2011 and the Gaspereau River during 2011.

Model	QAICc	Delta QAICc	QAICc weights	No. of Parameters	QDeviance
Gaspereau 2011					
S (CON) p (CON)	105.9	0.0	0.91	2	36.1
S (REC) p (CON)	112.0	6.1	0.04	8	28.1
S (CON) p (REC)	112.2	6.3	0.04	8	28.2
S (REC) p (REC)	116.0	10.1	0.01	13	17.9
Stewiacke 2008					
S (GROUP) p (REC)	215.8	0.0	0.52	10	59.0
S (CON) p (REC)	216.2	0.4	0.43	7	66.2
S (GROUP + REC) p (REC)	221.2	5.4	0.04	14	55.0
S (REC) p (REC)	222.6	6.8	0.02	11	63.5
S (GROUP + REC) p (CON)	242.8	26.9	0.00	10	86.0
S (GROUP) p (CON)	243.3	27.5	0.00	5	97.6
S (CON) p (CON)	244.4	28.6	0.00	2	105.1
S (REC) p (CON)	245.0	29.2	0.00	7	95.0
S (GROUP + REC + GROUP:REC) p (REC)	252.3	36.5	0.00	29	45.4
S (GROUP + REC + GROUP:REC) p (CON)	273.7	57.9	0.00	25	78.6
Stewiacke 2011					
S (CON) p (REC)	122.2	0.0	0.41	11	35.2
S (GROUP) p (REC)	122.8	0.6	0.30	12	33.4
S (REC) p (CON)	123.7	1.6	0.19	11	36.8
S (GROUP + REC) p (CON)	125.4	3.3	0.08	12	36.1
S (CON) p (CON)	129.7	7.6	0.01	2	62.8
S (GROUP) p (CON)	130.8	8.7	0.01	3	61.8
S (REC) p (REC)	131.1	8.9	0.00	19	23.9
S (GROUP + REC + GROUP:REC) p (CON)	132.7	10.5	0.00	20	22.7
S (GROUP + REC) p (CON)	137.4	15.2	0.00	21	24.7
S (GROUP + REC + GROUP:REC) p (REC)	149.2	27.0	0.00	29	12.5

Note: Models estimate survival (S) and detection probability (p). Parameters were modelled using the following explanatory variables: receiver (REC) or a constant effect (CON, i.e., a single parameter for all receivers), a release group effect (GROUP) and their interactions. Models are ranked based on second-order, quasi-likelihood Akaike information criterion (QAICc).

Fig. 2. Standardized survival estimates ($S\cdot\text{km}^{-1}$; solid circle ± 95% confidence intervals) as a function of distance from the head-of-tide (km) for Atlantic salmon smolts in the Gaspereau River during 2011 (*a*) and in the Stewiacke River during 2008 (*b*) and 2011 (*c*). Estimates are from weighted model averaging for each data set. The solid line (panels *a* and *b*) shows the cumulative survival as smolts migrate downstream. In panels *b* and *c*, the solid line denotes the cumulative survival of release group 1, and the dotted line denotes the cumulative survival of salmon in release group 2. Release groups 3 and 4 not shown for the 2008 Stewiacke data (panel *b*). The approximate area of striped bass spawning grounds is denoted by grey shading. The head-of-tide is indicated by the vertical dashed line.

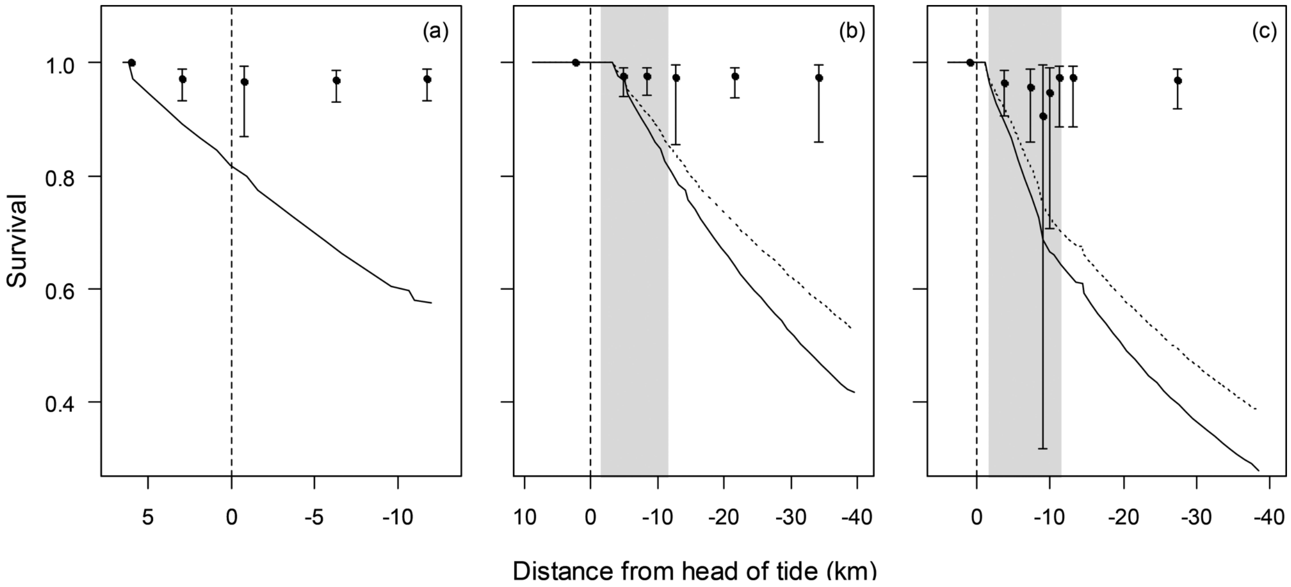


Fig. 3. Results of hierarchical clustering analyses of the migration metrics of Atlantic salmon smolts (S##) and striped bass (B##) in the Stewiacke River during 2008 (*a*) and 2011 (*b*). Smolts preceded by a solid circle indicate those tags detected at the mouth of the estuary.

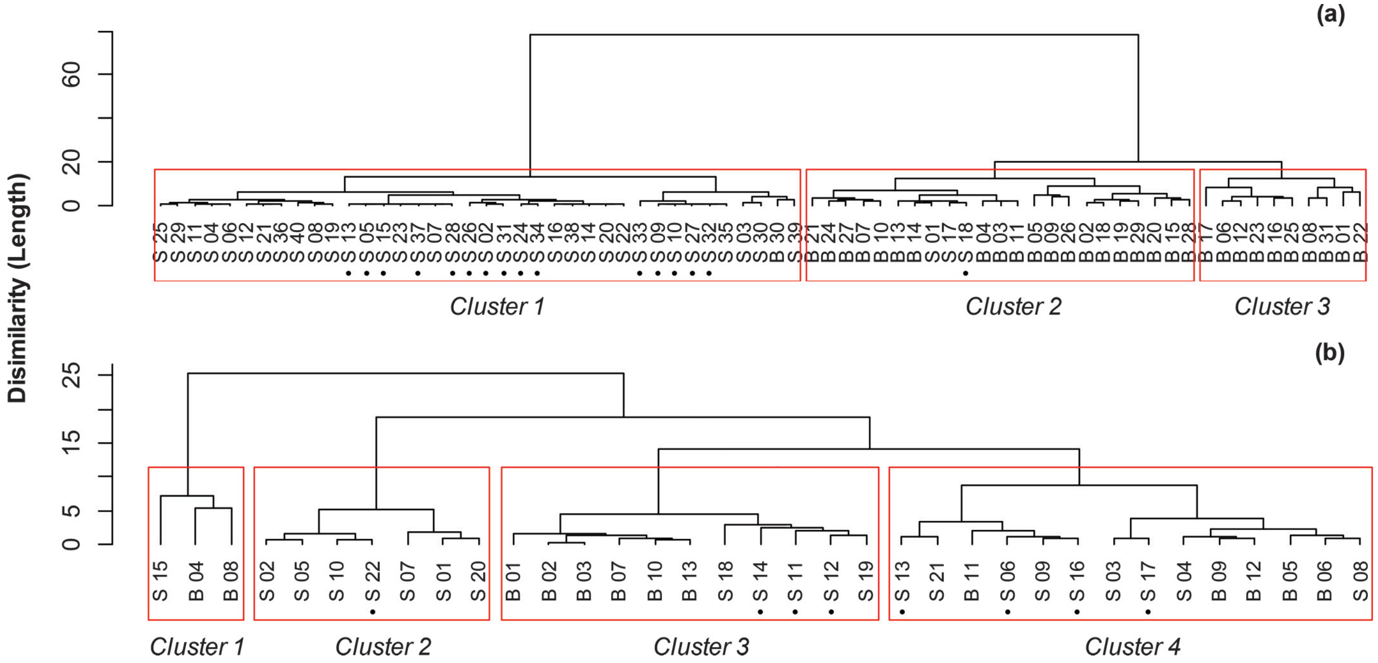


Fig. 4. Examples of the movement patterns (distance from the head-of-tide versus time) of tags placed in Atlantic salmon smolts (S##) and striped bass (B##) within the lower Stewiacke River, its estuary, and the lower Shubenacadie estuary, during 2008. Columns correspond to each cluster shown in Fig. 3*a*. Solid circles at the end of tracks indicate when a tag was detected at the mouth of the estuary. The dashed horizontal line indicates the head-of-tide, and the shaded band shows the approximate spawning grounds of striped bass.

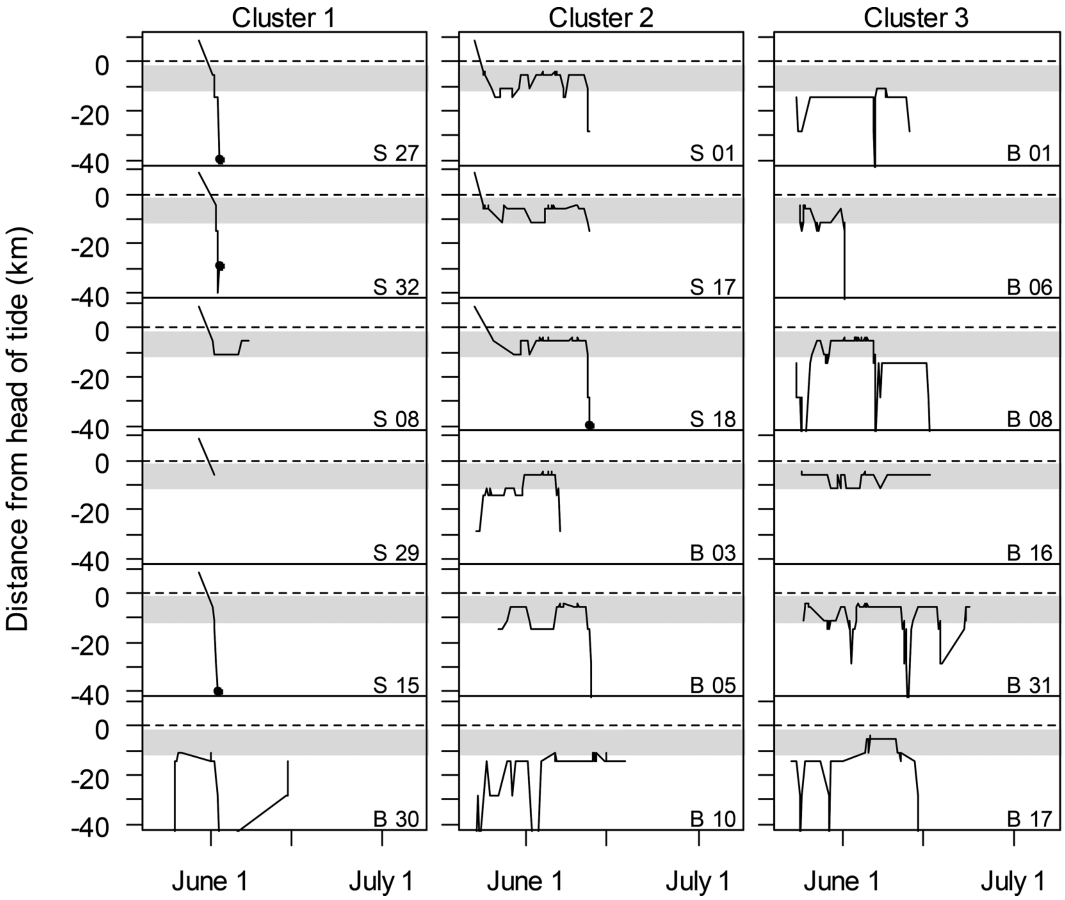


Table 4. Median and range (in parentheses) of the migration metrics for each of the three major behavioural clusters identified for Atlantic salmon smolt and striped bass in the Stewiacke River in 2008.

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 (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)
Time on spawning grounds (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^{-1})	0.0 (0.0–1.8)	0.3 (0.1–0.8)	1.2 (0.2–3.2)
Maximum upstream speed (m·s^{-1})	0.0 (0.0–4.8)	1.0 (0.2–3.4)	5.1 (0.4–19.1)
Mean downstream speed (m·s^{-1})	0.4 (0.1–0.9)	0.5 (0.2–1.6)	1.2 (0.5–2.3)
Maximum downstream speed (m·s^{-1})	1.3 (0.1–2.5)	1.5 (0.3–11.4)	7.0 (3.8–18.1)

Note: Cluster 1 contains primarily Atlantic salmon smolts, cluster 2 contains primarily striped bass but also three salmon, and cluster 3 contains exclusively striped bass. Clusters are reported in order they appear from left to right in Fig. 3*a*.

Table 5. Median and range (in parentheses) of the migration metrics for each of the four major behavioural clusters identified for Atlantic salmon smolt and striped bass in the Stewiacke River in 2011.

Metric	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Total displacement (km)	201.2 (180.0–229.5)	18.4 (5.6–43.7)	83.4 (49.5–136.7)	37.9 (22.3–71.3)
Total time (days)	33.0 (30.0–40.1)	8.0 (5.4–12.6)	10.7 (8.7–20.9)	6.4 (4.2–19.2)
Total detections	3518 (1333–11 546)	2003 (97–369)	1186 (591–3854)	500 (177–1120)
Total days with detections	27 (21–34)	4 (3–6)	12 (10–21)	5 (3–7)
Total number of reversals	28 (28–42)	0 (0–1)	14 (8–19)	5 (1–8)
Time on spawning grounds (days)	15.6 (7.0–32.0)	0.5 (0.0–2.1)	8.7 (3.3–13.9)	2.4 (0.3–4.7)
Mean upstream speed (m·s^{-1})	0.6 (0.5–1.0)	0.0 (0.0–0.4)	0.6 (0.3–0.7)	0.8 (0.3–1.4)
Maximum upstream speed (m·s^{-1})	1.7 (1.6–1.8)	0.0 (0.0–0.4)	1.2 (0.8–1.6)	1.2 (0.5–1.7)
Mean downstream speed (m·s^{-1})	0.6 (0.5–0.6)	0.3 (<0.1–0.5)	0.3 (0.2–0.4)	0.4 (0.2–0.6)
Maximum downstream speed (m·s^{-1})	3.9 (1.3–6.7)	0.8 (<0.1–1.6)	1.1 (0.7–1.6)	1.3 (0.6–2.1)

Note: Cluster 2 contains only Atlantic salmon smolts; the other clusters contain both striped bass and salmon. Clusters are reported in order they appear in from left to right in Fig. 3*b*.

as the spawning grounds (or one 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 the 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 (Fig. 3*b*) generally exhibited prolonged residency on the spawning grounds with more frequent migration reversals and longer detection histories (although shorter than the tags identified in cluster 1). Conversely, cluster 4 (Fig. 3*b*) was typified by tags that exhibited relatively few reversals, minimal time on the spawning ground, and relative short detection histories (Table 5). Based on these observations, in 2011, the fate of the three smolts in cluster 3 were reassigned from having successfully exited the estuary to having died.

In 2008, 41 smolts were included in the CJS analysis, one of which was reclassified as having died based on the cluster analysis. In 2011, 22 smolts were included in the CJS analysis, three of which were reclassified as having died based on the cluster analysis. The predation-bias adjustments for 2008 and 2011 are therefore 0.024 and 0.136, respectively. The effect of applying these adjustments to the CJS analysis was to reduce the estimated survival from 43.5% to 41.1% in 2008 and from 32.6% to 19.0% in 2011.

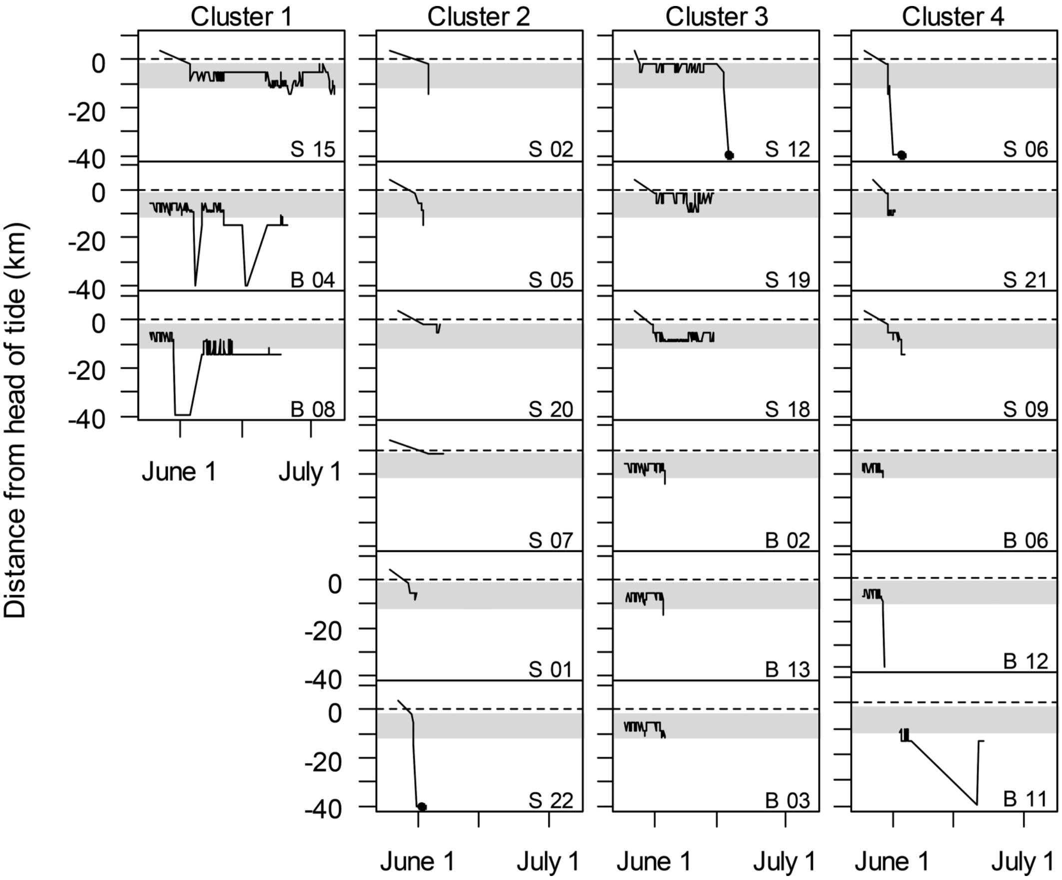
Discussion

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. Failing to consider the potentially confounding effects of predation can lead to misinterpretation of telemetry data and, ultimately, to inaccurate estimates of fish movement, behaviour, and survival. Unexpected tag movements have been previously interpreted as evidence of predation (e.g., Beland et al. 2001; Thorstad et al. 2011*a*; Melnychuk et al. 2013); however, there have been few attempts to quantify the impact of this predation on survival estimates. Both Perry et al. (2010) and Buchanan et al. (2013) interpreted abnormal and unexpected upstream migration of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) as evidence of predation and either manually censored these fish from survival models or manually truncated their individual detection histories to improve survival estimates. However, this approach is heavily reliant on the subjective identification of predation events based on what is perceived to be abnormal behaviour. In an effort to increase autonomy and reduce the subjectivity of the identification of predation, Romine et al. (2014) were able to successfully contrast predator and prey movements using high-resolution three-dimensional telemetry data collected over a small spatial scale and a finite mixture model. Although survival estimates were not reported by the authors, this approach could greatly improve survival estimates in 3D telemetry arrays.

Our study contributes to this research by quantifying the confounding effect of predation on acoustic telemetry-based survival estimates, thereby highlighting the potential bias associated with failing to identify predation. For Stewiacke River smolts in 2011, the CJS survival estimate was approximately 50% higher than the same estimate adjusted for predation effects. In addition, our approach was applied to using a two-dimensional telemetry system at a large spatial scale, a common arrangement of telemetry systems.

Fig. 5. Examples of the movement patterns (distance from the head-of-tide versus time) of tags placed in Atlantic salmon smolts (S##) and striped bass (B##) within the lower Stewiacke River, its estuary, and the lower Shubenacadie estuary, during 2011. Columns correspond to each cluster shown in Fig. 3*b*. Solid circles at the end of tracks indicate when a tag was detected at the mouth of the estuary. The dashed horizontal line indicates the head-of-tide, and the shaded band shows the approximate spawning grounds of striped bass.



The purpose of the cluster analyses of the tag movement characteristics 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 of 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 substantial differences in body size (smolt length approximately <0.2 m versus striped bass length approximately 0.4–0.9 m) and purpose of migration. Atlantic salmon smolts are generally thought to transit estuaries rapidly en route to marine habitats (Hansen and Quinn 1998; Thorstad et al. 2011*b*), while striped bass in this area are primarily spawning (Douglas et al. 2003), but also apparently foraging. Therefore, our assumption that migration patterns that are similar between salmon smolt tags and striped bass represented a predation event may be reasonable. Clear breaks among different movement patterns were well supported by the cluster analyses even though identification of number of important clusters, as well as the interpretation of clusters, was partially subjective. Clustering results in 2008 conformed to expectations regarding predation 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.

The 2011 data were considerably more difficult to interpret, largely owing to the increased variability in striped bass behaviour. Only one cluster (No. 2) contained exclusively salmon smolts, while the other three contained a mixture of species. We interpreted salmon in one of these clusters (No. 3) as evidence of predation, while the remaining cluster was interpreted as salmon plus striped bass with less extensive detection histories compared with other striped bass. An alternative interpretation of this cluster is that these salmon also represent predation events that would further reduce overall smolt survival (to near zero) and increase the estimated predation rate. The number of tags reclassified as "depredated–died" could be underestimated given that the migration parameters used in the cluster analyses represented the summary values across the entire movement track for each individual. Only those tags that were consumed early enough would be expected to demonstrate substantial changes in these values. If predation occurred late (i.e., near the end of the series of detections), the metrics for smolt tags would reflect predominantly smolt movements and thus would be expected to cluster with other smolt tags. Additionally, it is not possible to identify the timing of predation (i.e., when detections switch from representing smolts to striped bass) from these cluster-based analyses. 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 occurrence of predation). Therefore, the results of these cluster analyses can only be used to offset cumulative CJS survival estimates or ratio-based estimates.

It is also possible that predation by striped bass contributes to the mortality rates estimated from tag disappearances as well, because of the unknown retention time of acoustic transmitters within the gastrointestinal tracts of striped bass. Data from other predatory species suggests that tag retention is 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). 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.

With respect to effects of predation on acoustic telemetry-based survival estimates, it is presently unclear whether predation events can fully be identified via analyses of behaviours, particularly in the absence of clear, a priori knowledge of the differences in migratory behaviour. Without question, misclassification, either by incorrectly assigning depredated tags as live smolts or incorrectly assigning live smolts as depredated tags, would affect the magnitude of the predation bias. Even if the behavioural differences are known, if predation events occur late during the migration, misclassification can still occur because the majority of the track would still resemble that of a smolt. 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 CJS 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. Reduction of the size of the sensor tags capable of identifying predation events (e.g., Béguer-Pon et al. 2012; Lacroix 2014; Wahlberg et al. 2014) would be important for telemetry studies on juvenile fishes such as salmon smolts. Further, the development of new sensor tags capable of specifically identifying predation events should be a priority and would permit more direct observation of predation rather than having to infer predation events from movement characteristics.

Predation can also have an effect on quantification of fish behaviour. For example, 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 days (n = 6, standard deviation (SD) = 6.8 days); however, after removing those tags suspected to be in striped bass, residency estimates are reduced to 5.5 days (n = 4, SD = 1.2 days).

Implications for the recovery of iBoF salmon

It has been suggested that many iBoF salmon populations exhibit localized residency within the Bay of Fundy (Jessop 1976; Ritter 1989; Amiro 2003), and telemetry of postsmolts 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). Additionally, 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 suggest that postsmolts exited the Minas Basin rapidly, and the detection of three Gaspereau River smolts on the Halifax line of receivers between 17 and 26 days later suggests that at least a portion of the population continues their migration northward towards Newfoundland and Greenland. Differences between the two populations in the number of postsmolts detected at both the Minas Passage line and the Halifax line of receivers are consistent with the migration strategies thought to be used by these two populations.

The estimated survival rates reported in this study suggest that estuarine and early marine survival may vary among iBoF rivers and among 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 6), although some of the differences in survival rates would relate to the size of the estuary. One 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 Minas Basin. Striped bass are possibly the most common predator within this area, and although an abundance time series is not available for the Shubenacadie – Stewiacke rivers 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 5 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 increased[1]. Alternative explanations include interannual variability in return rates, which can vary by factors of three to five or more in some populations (Gibson and Bowlby 2013), and ongoing declines in at-sea survival for some other reason. For example, return rates for salmon in the Big Salmon River, New Brunswick (another iBoF population), declined from a mean of 4.7% during the 1966 to 1971 time period (Ritter 1989) to 0.3% for the 2002 smolt cohort (Gibson et al. 2004). Additionally, tag size effects cannot be discounted. Although the tags used by Lacroix (2008) in 2002 were heavier than the tags used in our study, the hatchery-reared smolts from the Stewiacke River in the 2002 study were larger than the wild-exposed smolts (hatchery-reared, but released as fry) used in 2011. As a result, the transmitter to smolt mass ratio in the 2011 study (mean = 10.0%) was higher than that in 2002 (mean slightly less than 7%). However, the transmitter to smolt mass ratios in 2008 (mean = 7.0%) were more similar to those used in 2002, although the resulting survival estimate was lower (49% in 2008 versus 69% in 2002).

The level of predation by striped bass estimated in this study for Stewiacke River smolts (7.3% in 2008 and 27.3% in 2011) is roughly 13% to 32% of the total mortality estimated to have occurred in the estuary (57.6% and 71.8% in 2008 and 2011, respectively). While we cannot preclude the possibility that all predation events were not accurately identified via the behavioural modelling, for example if predation occurs without the tag being consumed, these results indicate that although predation rates appear high enough to warrant consideration in recovery planning, other factors in addition to striped bass predation may be 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

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[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 voluntary information on marine fisheries conducted by licensed freshwater anglers and may not adequately describe catch trends.

Table 6. Summary of estimates for the estuarine survival of Atlantic salmon smolts in rivers of the Bay of Fundy (BoF), 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	W and H	Yes	CJS-predation	41%	This study
Stewiacke	2011	W and H	Yes	CJS-predation	19%	This study
Gaspereau	2011	W and H	Yes	CJS	57%	This study
Other studies on the Stewiacke or Gaspereau rivers						
Gaspereau	2002	H	Yes	KF[a]	69%	Lacroix 2008
Stewiacke	2002	H	Yes	KF[a]	80%[b]	Lacroix 2008
Other BoF rivers						
Upper Salmon	2001–2002	W and H	Yes	KF[a]	97%–100%	Lacroix 2008
Big Salmon	2001–2002	W and H	Yes	KF[a]	78%–96%	Lacroix 2008
Nashwaak	2002	W and H	Yes	KF[a]	56%–59%	Lacroix 2008
St. John	2001	H	Yes	KF[a]	44%–55%	Lacroix 2008
Southern Upland rivers						
Lahave	2010	W	Yes	CJS[a,c]	85%	Halfyard et al. 2013
Gold	2010	W	Yes	CJS[a,c]	89%	Halfyard et al. 2013
West, Sheet Harbour	2008–2010	W	Yes	KF[a,c]	54%–74%	Halfyard et al. 2013
St. Mary's	2010	W	Yes	KF[a,c]	83%	Halfyard et al. 2013
Gulf of Maine rivers						
Narraguagus (Maine)	1997–1999	W	No	CJS	60%–75%	Kocik et al. 2009
Narraguagus (Maine)	2002–2004	W	No	CJS	68%–74%	Kocik et al. 2009

[a] Estimates adjusted for handling mortalities.

[b] Receiver location at mouth of Shubenacadie estuary was upstream from location used in this study.

[c] Halfyard et al. (2013) report standardized survival (i.e., $S\cdot\text{km}^{-1}$); these estimates are the cumulative estimates to the mouth of the estuary. In all cases, survival was estimated to the seaward extent of the estuary only. Survival estimates were from the most upstream receiver in this study, and in some rivers reported by Lacroix (2008), but was from the site of release in all other estimates. CJS = Cormack–Jolly–Seber; KF = known fate.

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. For example, the smolt-to-adult return rate from the 2002 Gaspereau River smolt cohort (wild-reared) was estimated to be 0.8% (Gibson et al. 2004). Although smolt abundance has not recently been estimated, partial counts of the number of emigrating smolt averaged 1084 individuals from 2007 to 2011, and the number of adult salmon returning to the river has not exceeded four in the last 3 years, indicating that survival may now be even lower. Based on the number of tags detected at the Minas Passage in 2011, survival of Gaspereau River smolt to this line would be expected to be no less than 47% (because detection efficiency is unknown, but cannot be greater than one). Similarly, survival of Gaspereau smolt to the Halifax line would be expected to be no less than 20%. If the value of 0.8% is used as the total return rate, survival of salmon from the time they were detected at the Minas Basin line until they return to the river as adults would not be expected to exceed 1.7%, and similarly, their survival from the time they were detected at the Halifax line until their return to the river would not be expected to exceed 4%. If return rates are presently lower than they were for the 2002 smolt cohort, survival after being detected at these lines would be also be expected to be lower. Return rates for the Stewiacke River are unknown; however, if they are assumed to be similar to other iBoF salmon populations, the same logic applies. Survival from the time they are detected at the Minas Passage line until they return to the river to spawn would be also be low.

For these reasons, conservation measures aimed only at reducing salmon mortality within iBoF estuaries and the Minas Basin are not expected to produce substantial population responses. For example, for the Gaspereau River population, if estuarine mortality could be reduced by as much as 50% (i.e., before reaching the Minas Basin), marine return rates would increase from 0.8% to 1.1%. Even at this increased return rate, the probability of extirpation within three generations in the absence of supportive rearing for these populations would remain near 1 (Gibson et al. 2008). While the results of this study do not identify a source of mortality sufficiently large to account for observed declines, they do narrow the window when the most influential mortality is expected to occur.

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