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**Estimating consumption rate of Atlantic Salmon smolts
(*Salmo salar*) by Striped Bass (*Morone saxatilis*) in the
Miramichi River estuary using acoustic telemetry**

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- 1   Estimating consumption rate of Atlantic Salmon smolts (*Salmo salar*) by Striped Bass (*Morone saxatilis*)
2   in the Miramichi River estuary using acoustic telemetry
- 3   Jason Daniels, Gérald Chaput and Jonathan Carr
- 4   Jason M. Daniels and Jonathan Carr. Atlantic Salmon Federation, 15 Rankine Mill Road, Chamcook, NB,
5   Canada, E5B 3A9
- 6   Gérald Chaput. Fisheries and Oceans Canada, 343 University Avenue, Moncton, NB, Canada, E1C 5K4
- 7   Corresponding author: Jason M. Daniels (email: jdaniels@asf.ca, phone: (506) 529-1039)
- 8

Draft

Abstract

Differentiating detections of a telemetered fish from those of predators which may have consumed that telemetered fish presents problems and opportunities. Previous efforts to quantitatively classify predation events have had to rely on data from unknown states of fish (i.e. unsupervised learning techniques) with the consequence that model performance cannot be refined or compared to alternate models. We circumvent this limitation by analysing acoustic telemetry track data to differentiate movement patterns of tagged Striped Bass (*Morone saxatilis*) from those of Atlantic Salmon (*Salmo salar*) smolts which were known to not have been predated by Striped Bass over a three year period in the Miramichi River estuary. A random forests classification model (i.e. supervised learning technique) was used to differentiate the movement patterns of these two species and the model was applied to Atlantic Salmon smolt movement characteristics to provide an index of Striped Bass predation-derived mortality. The optimized random forests model inferred that predation rates by Striped Bass were highly variable between years for two smolt stocks, ranging from 1.9% to 17.5%. Spatial and temporal overlap of the two species is a likely factor defining the between stock and annual variation of predation rate estimates.

24 Introduction

25   Telemetry studies often assume that detections are from the individual tagged. This assumption is
26 violated when a tagged fish is consumed by a predator or scavenger and the tag continues to be
27 detected by acoustic receivers (Gibson et al. 2015). Miniaturization of acoustic transmitters is permitting
28 researchers to make inferences on survival and movement behaviour of increasingly smaller fish (Welch
29 et al., 2009), exasperating the issue of predation in telemetry studies. Biases in movement behaviour
30 and survival can be introduced if no attempt is made to differentiate between the detections of targeted
31 species of interest and those of possible predators. As acoustic telemetry became a more widely
32 adopted tracking method, classification of movement behaviours of presumed predated and presumed
33 unpredated fish evolved from observations (Beland et al. 2001), subjective and qualitative analyses
34 (Melnychuk et al. 2013) and, more recently, to quantitative approaches (Gibson et al. 2015; Romine et
35 al. 2014). Efforts to quantify predation events, however, have had to rely on data from unknown states
36 of fish otherwise termed unsupervised classification methodologies. This has primarily been due to the
37 absence of known states of the tagged individuals as either having been predated or not.

38   In the absence of data of known states of tagged individuals, model classification error cannot be
39 evaluated. Furthering the development of quantitative models, especially those capable of being
40 evaluated, presents several important implications: (1) they allow for the evaluation of model
41 performance and therefore competition between models, (2) they allow repeatable identification of
42 predated individuals and removal of their biased detection, and (3) they provide researchers with an
43 opportunity to study the impacts and extent of predation. Here we seek to build upon previous work by
44 using a classification method, based on detection histories, to identify acoustically tagged Atlantic
45 Salmon smolts (*Salmo salar*) that may have been consumed by Striped Bass (*Morone saxatilis*) in the
46 Miramichi River. We then use the results of this model to provide an index of predation derived
47 mortality on salmon smolts.

Striped Bass are found in estuaries and near-shore coastal waters along the eastern seaboard of North America. A distinct population in the southern Gulf of St. Lawrence (SGoSL) is considered to be the northern limit of the species range (Bradford and Chaput 1996). This population is broadly distributed and contained to the southern Gulf of St. Lawrence between the eastern tip of the Gaspé Peninsula (47°37' N; 64°09'W) to the western tip of Cape Breton (47°03' N; 60°36'W). The only annually predictable spawning location of this population is in the Northwest Miramichi River (46°57' N; 65°40'W). The abundance of spawners was at a very low point in the mid 1990s, with historical variations in abundance and declines largely attributed to fisheries (Bradford and Chaput 1996). Incremental management measures led to the closure of commercial and recreational fisheries from 1996 to 2000 (DFO 2014). Following the implementation of these management actions, the abundance of SGoSL Striped Bass on the spawning grounds increased from fewer than 5,000 fish in the mid-1990s to an estimated 318,000 fish in 2016 (DFO 2017). The Miramichi River estuary and bay is a well-known overwintering site for Striped Bass (Douglas et al., 2006; DFO 2014). Striped Bass spawn in the upper reaches of the Northwest Miramichi River estuary during late May and June (Douglas et al. 2006, 2009).

The Miramichi River also supports one of the largest runs of Atlantic Salmon in North America however the abundance of Atlantic Salmon in this river has declined over the past two decades much like Atlantic Salmon throughout the North Atlantic (Chaput 2012). Estuaries are considered to be areas with high mortality for salmon smolts due to the physiological stress associated with migration, anthropogenic stressors, and predation (Thorstad et al. 2012). Telemetry studies of Atlantic Salmon smolts have estimated a two-fold decline in apparent survival rates in the Miramichi estuary from the mid 2000s to recent years (2013-2016) but not in a neighbouring group of rivers in the SGoSL (Chaput, G., Daniels, J., Carr, J., Jonsen, I., and Whoriskey, F. In review). The decline in apparent survival rates of acoustically tracked salmon smolts in the Miramichi estuary has occurred concurrently with the recent large increases in Striped Bass spawner abundances in that area. The spawning aggregation of Striped

Bass overlaps spatially and temporally with the seaward migration of Atlantic Salmon smolts from the Miramichi River. Predation of Atlantic Salmon smolts by Striped Bass over a very narrow window of time corresponding to the migration period of salmon smolts has been confirmed from diet studies of Striped Bass in the Miramichi River area (DFO 2016).

While the increased abundance of Striped Bass in the SGoSL is unlikely to be the only factor contributing to the multidecadal decline of Atlantic Salmon in the Miramichi River and throughout eastern Canada, the extent of the inter-species interactions and their consequences during the initial migration period are poorly understood. In this study, we model differences in movement characteristics of Atlantic Salmon smolts and Striped Bass spawners using acoustic tag detections to estimate the proportions of tagged Atlantic Salmon smolts that may have consumed by Striped Bass. We compiled a data set consisting of 'true' smolt and 'true' Striped Bass movement behaviours to first train a random forests model (a supervised classification technique; Breiman 2001), to differentiate between the two species' movement characteristics. The objective of this study was to apply the model predictions to movement patterns of acoustically tagged smolts to determine which Atlantic Salmon smolt patterns whose true state was not known had acoustic tracks which were more similar to those of Striped Bass and thus could be interpreted as a probable predation event. Using the classification model, estimates of the proportion of acoustically tagged Atlantic Salmon smolts presumably consumed by Striped Bass in the Miramichi River are estimated annually from 2013 to 2016. To confirm the extent of the spatial and temporal overlap between tagged Striped Bass and tagged Atlantic Salmon smolts in the Miramichi estuary, we present an estimate of the percentage overlap between the two species.

METHODS

Field study

Description of the Miramichi river system

The Miramichi River system has a catchment area of roughly 14,000 km² (Fig. 1). There are two main branches of the Miramichi River; the Northwest Miramichi River (NW) and the Southwest Miramichi River (SW) which both drain into a single estuary that enters the SGoSL at latitude 47°N (DFO 2013). The Southwest Miramichi River is the larger of the two branches with over double the mean yearly discharge (177 and 86 m³s⁻¹ comparatively). The lower portions of both branches are under tidal influence.

Description of the tagging protocols

Atlantic Salmon smolts

Two stocks of Atlantic Salmon smolts were collected using rotary screw traps, located at Rocky Brook Salmon Camp for the SW (46.600481°N, 66.632079°W) and at the NW (47.094277°N, 65.837024°W) (Fig. 1). Smolts ≥13 cm fork length were preferentially selected to accommodate the acoustic transmitter. Vemco V9-6L acoustic transmitters (9 mm diameter by 21 mm length, 2.9 g in air) were used in 2013 and 2014. We began to transition to smaller V8-4L (8 mm diameter by 21 mm length, 2 g in air) acoustic transmitters in 2014 and they were used exclusively in 2015 and 2016. In all years, acoustic transmitters were uniquely coded and programmed to emit signals at random time intervals between 25 s and 55 s at a frequency of 69 kHz. Before each surgery tag activation was confirmed with a Vemco VR100 mobile acoustic receiver (Amirix/Vemco, Bedford, Nova Scotia, Canada).

All smolts selected for surgery were held in in-stream tanks for 20 to 24 hours to allow for digestion of stomach contents. At the SW, smolts were released approximately 100 m downstream of the screw trap at the confluence of the SW Miramichi and Rocky Brook. At the NW, smolts selected for

surgery were transported in an oxygenated 1 m³ insulated HDPE tank. The surgery and release location (47.187224°N, 65.89506°W) was located approximately 13 km upstream from the rotary screw trap.

Smolts were anaesthetised using clove oil (0.2 ml L⁻¹ concentration) until loss of equilibrium and very little gill movement (generally 3-5 minutes). Once this had occurred, fork length (cm) was taken before the fish was placed ventral side up on a v-shaped operating board lined with a chamois leather. All surgical tools and tags were disinfected in anhydrous ethyl alcohol prior to each surgery, before being rinsed in distilled water. An approximately 11 mm incision was made along the mid-ventral line about 20 mm anterior to the pelvic girdle. Acoustic transmitters were inserted via the incision into the abdominal cavity of the fish. The fish's gills were continuously irrigated with a wash bottle containing anaesthetic during the surgery. The fish's body was kept moist throughout the surgery by using a wash bottle containing river water to irrigate the skin, avoiding the incision area. Incisions were sealed using 2 to 3 interrupted stitches using 4/0 non-absorbable black monofilament nylon sutures with 19 mm reverse cutting blades. Fish were placed in an aerated recovery bath for observation. Once equilibrium had been restored, fish were transferred to in-river holding tanks at the respective release sites, and held for a minimum of one hour before release.

During 2013 to 2016, a total of 514 Atlantic Salmon smolts were acoustically tagged and released in the Miramichi River (Table 1). Of these, 374 smolts were subsequently detected between head of tide receivers and Miramichi Bay exit receivers. The mean fork length of smolts selected for acoustic tags was 14.2 cm within a range of 12.1 cm to 18.2 cm (Table 1). Surgery/release dates ranged between May 10 and May 30 with a mean surgery/release date of May 21 over all years.

Striped Bass

In October 2013, a total of 40 Striped Bass were selected from catches at the Department of Fisheries and Oceans Canada (DFO) index estuary trapnet in the Southwest Miramichi River (46.600481°N, 66.632079°W). Details of the trapnet operation are given in Hayward et al. (2014). The Striped Bass

139 tagged in 2013 were collected between October 10 and 21. The tagged bass had a mean fork length of
140 58.8 cm, with a range of 45.6 to 73.5 cm. The acoustic tags used were a combination of Vemco V16T-4L
141 and V16TP-4L configured with a random ping interval between 60 and 180 seconds. Striped Bass from
142 the daily catches were retained in the trapnet holding area, and transferred to shore in small numbers
143 for tagging. Tagging and handling procedures were as described by Douglas et al. (2009). Some of these
144 tagged bass overwintered in the tidal waters of the Miramichi River and were tracked in the spring onto
145 the spawning grounds until they left the area. A large number of these fish returned in subsequent fall
146 months of 2014 and 2015 to overwinter and participated in spawning during the springs of 2014 to 2016
147 (DFO 2015, 2016).

148 In late summer 2013, the Ministère des Forêts, de la Faune et des Parcs, province of Quebec,
149 acoustically tagged Striped Bass captured along the north shore of Chaleur Bay to determine the
150 movements of Striped Bass at the northwest extent of the defined geographic distribution of the
151 southern Gulf of St. Lawrence population. Striped Bass were collected by angling. A total of 50 bass were
152 sampled and tagged with Vemco V13 acoustic transmitters configured with a random ping interval
153 between 60 and 180 seconds. Tagging and handling methods were consistent with DFO methodology.
154 Of the bass acoustically tagged in this area, 38 were detected in tidal waters of the Miramichi River pre-
155 winter 2013 to 2016.

156 *Description of the receiver deployment:*

157 Hydro acoustic receivers (Amirix/Vemco, Bedford, Nova Scotia, Canada, VR2W models) were
158 deployed within the Miramichi river system and Gulf of St Lawrence to record smolt passage (Fig. 1). For
159 this study, 7 receivers were moored in the NW, 5 in the SW, and 5 in the mainstem Miramichi. The outer
160 bay array (where Miramichi Bay joins the Gulf of St Lawrence) consisted of 11 receivers and the Strait of
161 Belle Isle (SoBI) array consisted of 24 receivers. All receivers were deployed in consistent locations
162 between 2013 and 2016 apart from an additional 28 receivers deployed approximately 3.5 km north of

the SoBI array in 2015 and 2016 to assess the detection efficiency of the SoBI array (Fig. 1). All receivers were attached to moorings consisting of varying weight anchors (depending on current and possible surface conditions), line and surface floats. In shallow reaches of the NW and SW, receivers were attached approximately 1 m below the surface floats whereas moorings in deeper water had receivers attached approximately 4 m below the surface floats. Sinking line was used from the surface floats to a nylon swivel located below the receiver, which in turn was attached to the anchor with floating line.

Statistical analyses

Behavioural classification

The movement patterns of Striped Bass were described directly from the tracking data as there is no reason to believe that a tag originally placed in a Striped Bass would have ended up in another fish species as there are no known fish predators of sufficient size in the Miramichi that could consume the Striped Bass tagged in this study.

We assumed that tags originally placed in Atlantic Salmon smolts that were subsequently detected at the Strait of Belle Isle array arrived there in post-smolts and not in any other aquatic species. As such the movement patterns of these Atlantic Salmon smolts were considered to be those of 'true' tagged Atlantic Salmon smolts which had not been predated upon by Striped Bass or any other fish predator.

In three of four years, detection data from concurrent Striped Bass and smolt migration studies were acquired. Movement patterns of 'true' smolts were described from the smolt tagging experiments of 2013 to 2016. The movement patterns of Striped Bass were described from the tracking data during 2014 to 2016. Detections of Striped Bass and Atlantic Salmon smolts were recorded on the common acoustic receiver deployments with the study period for each year (i.e period between the first and last detection of any smolt transmitter in the Miramichi River).

Eight variables characterizing movement patterns were generated based on similar criteria to those of Gibson et al. (2015). These variables included: (1) average speed through system, (2) time between first and last detection within the study period, (3) count of switches in upstream and downstream movement direction, (4) cumulative upstream distance between receiver detections, (5) cumulative distance between receiver detections, (6) time on defined bass spawning grounds (between the 57 and 69 kilometer mark on the Northwest Miramichi River), (7) time between first and last detection on defined bass spawning grounds, and (8) count of visits and switches between the Northwest and Southwest Miramichi Rivers. These variables adequately differentiated the two species movement patterns based on descriptions of Douglas et al. (2009) and Kocik et al. (2009).

Detection data for each transmitter were truncated to the first detection on the last receiver that the transmitter was detected on. This censoring was done to avoid potential variable bias as some transmitters were continuously detected at a single receiver over an extended period of time (i.e. the transmitter stops moving). This is likely due to the mortality of a tagged fish or tag expulsion within the detectable range of the receiver.

Random forests (RF) models to differentiate between the two species' movement patterns were constructed (see Cutler et al. 2007 for random forest description) using the "*randomForest*" package (Liaw and Wiener 2002) in program R (R Core Team). Inferences of the proportions of acoustically tagged Atlantic Salmon smolts that had movement patterns characteristic of Striped Bass were obtained as follows: (1) variables describing the movements of the two species were developed, (2) a dataset of 'true' salmon and bass was compiled to train the RF model to differentiate between smolt and bass movements, (3) the inferences of the RF model were optimized by using k-fold cross validation to choose a set of randomly selected predictors within each tree of the RF model, (4) the RF model structure based on the training set was applied to all smolt detection data during the study period, to estimate the probability of an individual smolt data track being either most similar to smolt behaviour or

bass behaviour, and (5) by stock and year, the estimated percentages of tagged smolts exhibiting probable Striped Bass movement patterns were compiled.

Movement patterns of individuals from each species with known states were required to train the RF model to differentiate between smolt-like and bass-like movements. To classify movement patterns in a supervised method it was assumed that: (1) transmitters implanted in Striped Bass are representative of 'true' Striped Bass movements and (2) transmitters implanted in Atlantic Salmon smolts that were detected at the Strait of Belle Isle (SoBI) receiver gate are representative of 'true' smolt movements within the Miramichi River. Detection data from both the SoBI and the Ocean Tracking Networks' (OTN) Cabot arrays suggest that SoBI is the primary point of exit of salmon smolts from the Gulf of St. Lawrence. The SoBI gate is located at the extreme northern limit of the GoSL, roughly 780 km from the mouth of the Miramichi River (Fig. 1). Shultz et al. (2015) examined the evacuation rates of acoustic tags from prey ingested by Striped Bass and reported a mean evacuation time of 1.8 days and a negative association with temperature. Given that the SoBI receiver gate is well beyond the defined known range of Striped Bass (DFO 2015) and the amount of time (30 to 61 days; Chaput, G., Daniels, J., Carr, J., Jonsen, I., and Whoriskey, F. In review) an ingested acoustic tag would need to remain in the gastrointestinal tract of a predator migrating to and detected at the Strait of Belle Isle, we believe our second assumption to be robust.

Model Optimization and Performance

Within the *randomForest* function the number of randomly selected variables (i.e. *mtry*) used for each tree was optimized. We defined the potential number of variables equal to the total number of descriptive variables (8). To select the optimal number of variables, ten-fold cross validation was used to resample the data, fit a model, and estimate the mean and 95% confidence interval of the Kappa statistic as per Kuhn and Johnson (2013). The Kappa statistic addresses the accuracy that would be expected by chance (i.e. accounts for imbalance between classes) and takes values ranging from -1 to 1.

Values of 1 indicate perfect agreement whereas a value of 0 represents agreement expected by chance alone (Viera and Garrett 2005). Among candidate models with differing *mtry* values, the model with the optimal Kappa value was selected. The *mtry* value from this optimal model was then used to refit the model using all data.

Model Application

For all acoustic transmitters implanted into smolts that also had detections (Table 1) within the study site, the optimal RF model was applied to generate the probability of each transmitter detection data exhibiting Striped Bass and smolt movement patterns (i.e. probabilities of both classes sum to one for each transmitter). Probabilities generated through the RF model reflect the proportion of trees within the forest with votes for the respective classes. A smolt track was assigned to smolt or bass categories using three approaches. First, a binary classification corresponding to a cut-off value of 0.5 with values ≤ 0.5 being a smolt pattern and > 0.5 being a bass pattern. Second, a scaled estimate, which is the sum of individual bass classification probabilities of each smolt tag divided by the total number of smolt tags modelled. This scaled estimation accounts for uncertainty in the assignment to either classification. Third, we present a three-level classification where we chose an arbitrary probabilistic cut-off with values ≤ 0.20 classified as a smolt pattern, ≥ 0.80 classified as a bass pattern and probability levels in between belonging to an 'unknown' state. The estimated percentage of inferred tagged smolts predated by Striped Bass was the number of smolts assigned to the bass category divided the total of smolts with detections for each smolt stock and year.

Spatial and temporal overlap

Two-dimensional kernel utilization distributions (KUDs) and the overlap at the 95th isopleth were calculated to quantify the extent of spatial and temporal overlap in the estuary area of the Miramichi between Atlantic Salmon smolts and Striped Bass. Geographic location was defined along a single dimension, the upstream distance of the detection. Smolts used to define the spatial and temporal

distribution field were those inferred to exhibit smolt behaviours as defined from the binary classification of the RF model. To calculate KUD overlap of NW smolts to those of Striped Bass, smolt and bass detections on the Northwest and mainstem Miramichi River receivers were used. The Southwest and mainstem Miramichi River receiver detections were used to calculate overlap of SW smolts and bass. Day of the year served as the temporal dimension in the analysis. Points within these two dimensions were estimated using each transmitter's mean upstream distance by day. KUDs were created using the "ks" package (Duong 2007) in program R (R Core Team). Bandwidth selection was performed using smoothed cross-validation. The percent of the area of each smolt KUDs occupied by the area of the corresponding bass KUDs, each truncated to the 95th isopleth, was calculated for the years 2014 to 2016 (Cooper et al. 2014; Simpfendorfer et al. 2012).

Results

Movement patterns of tagged Atlantic Salmon smolts detected at SoBI and of tagged Striped Bass were pooled across all years to train the RF model. Detection data used to characterize Striped Bass movements were assembled from a total of 228 bass; 66 bass in 2016, 80 bass in 2015, and 82 bass in 2014. Detection data of 'true' smolt movement patterns were compiled for 63 individuals; 16 smolts in 2016, 28 smolts in 2015, 12 smolts in 2014, and 7 smolts in 2013. A 'true' salmon smolt movement pattern was typically characterized by unidirectional downstream movements (Fig. 2 a,b,c,d) and 'true' Striped Bass movement patterns had more frequent up and downstream reversals (Fig. 2e). No Striped Bass detection data were available for 2013, however we included smolt detection data from this year because several smolts detected at the SoBI gate exhibited more variable in-river movement patterns in that year compared to the other years (e.g. Fig. 2b). There was no evidence to suggest that Striped Bass had annual variations in movement patterns. Inclusion of the 2013 smolt detection data allowed for a greater range of 'true' smolt movement patterns to be included in the training data set to derive the final and optimal classification model (Fig. 3). Due to an inconsistent number and deployment location

of receivers in the Miramichi River system, no data are available prior to 2013 to train and/or apply predictions of the model.

Random forest models were trained across the range of eight potential variables and each RF model consisted of 10,000 trees. The optimal number of randomly selected variables selected for each tree in the random forest was five. This optimized model had a Kappa value of 0.989 (s.d. 0.036). The final model had a classification error of 0.0 for the Striped Bass classification and 0.016 for the smolt classification (one smolt was classified as having movement patterns most similar to Striped Bass). This high degree of classification accuracy on the training data was somewhat expected given the considerable differences between species for the movement variables used (Fig. 3).

Applying the optimized RF model to all smolts acoustically tagged and subsequently detected in the Miramichi estuary provided inferences on the proportions of tagged smolts which exhibited Striped Bass movement patterns. The distributions of these probabilities for each stock and year are presented in Figure 4. Given the generally bimodal distribution near 0 and 1 for these classification distributions, this approach demonstrates that the characterization of tagged smolt movements can be classified with a reasonable degree of certainty. The percentages of smolt tags predicted to have movement patterns in the Miramichi estuary that are characteristic of Striped Bass tags and by inference were consumed by bass (i.e. binary classification estimate) are presented for each stock and year of the study (Table 1). To account for any uncertainty in the classification both the scaled estimate and the percentages of smolt tags with a classification probability ≥ 0.80 are also presented in Table 1. Using the scaled estimate across all year's predictions (i.e. 2013 to 2016), tagged smolts from the NW were characterized more frequently as showing Striped Bass movement patterns (15.3%) than tagged smolts from the SW (8.6%). Defining states of smolt tags under the three-level classification scheme (i.e. smolt, unknown or bass) presents slightly lower estimates for 2013 and 2016, compared to estimates using the binary classification scheme. Perfect agreement between the binary and three-level classification schemes was

present for 2014 and 2015. For most years and stocks, few tagged smolt movement patterns were defined as belonging to an unknown state, ranging from 2.0% to 8.3% for NW smolt tags and 0.0% to 10.7% for SW smolt tags (Fig. 5).

The spatial and temporal overlap between Striped Bass and Atlantic Salmon smolts based on tag detections varied annually in the Miramichi estuary but it was estimated to be greater for Northwest smolts than for Southwest smolts (Fig. 6). Striped Bass congregated most densely in the NW estuary in all years (Fig. 6). In 2014 and 2015 Striped Bass congregated in the mainstem Miramichi before spawning and during the tagged smolt migration period, however, this was not apparent in 2016 (Fig. 6). Most tagged smolts passed through the Miramichi estuary over a two-week period, typically from last week of May to the first week of June (Fig. 6). The spatial and temporal overlap between SW Miramichi tagged Atlantic Salmon smolts and tagged Striped Bass ranged from 18.7% to 56% (Fig. 6), whereas the spatial and temporal overlap between NW Miramichi smolts and Striped Bass ranged from 45.3% to 70.7% (Fig. 6). Spatial and temporal overlap between Striped Bass and both smolt stocks was lowest in 2015.

Discussion

Two previous studies (Gibson et al. 2015; Romine et al. 2014) attempted to use quantifiable methods to estimate the number of consumption events using acoustic telemetry data and both studies considered salmonid and Striped Bass interactions. These studies were limited to unsupervised learning (i.e. clustering) algorithms (which hierarchically organize data based on similarity) because they had no information on movements of prey fish of known states. In both studies, it was assumed that Striped Bass movement patterns represented 'true' Striped Bass patterns and these were used to validate the clustering of Striped Bass. Romine et al. (2014), however, raised the issue of being unable to validate smolt classifications due to the infeasibility of recapturing smolts to confirm their true state (i.e. predated or not). Given that unsupervised techniques model the underlying structure of the data, model performance cannot be evaluated (i.e. classification error). This implies that the model generated

cannot be refined or compared to alternate (i.e. competing) models to select an optimal classification model.

Here we circumvented this limitation by having data on potential predator movements and concurrent data on potential prey movement patterns that escaped predation and this information was used to guide a supervised learning technique, random forests. Many studies have outlined the enhanced prediction accuracy of supervised over unsupervised classification techniques (Guerra et al. 2011; Rozenstein and Karnieli 2011; Venkatesan and Kulkarni 2016). The training data set developed under these assumptions proved to be a near perfect classifier with one misclassification (a smolt classified as striped bass) of 63 'true' movement tracks (1.6% misclassification rate).

While we have demonstrated that this methodology improves upon existing approaches to classify movement patterns, there are limitations. The presentation of the scaled consumption estimates provides an indication of the degree and direction of uncertainty in the estimated probability of smolt consumption events. In all but two cases (2013 SW smolts, 2016 NW smolts) the scaled estimate is greater than that of the binary output suggesting that the binary classification estimates may underestimate potential predation events. Gibson et al. (2015) remarked, through a similar analysis, on the limitations due to the quantification of movement characteristics across the extent of the study period. The greater the amount of time a consumed smolt tag remains in a Striped Bass the more likely the model is to identify the movement pattern as Striped Bass. On the other hand, smolt movement patterns that deviate from the typical patterns of smolts detected at SoBI are also more likely to be assigned as Striped Bass consistent patterns, such as the example outlined in Figure 2b.

While this methodology could include multiple states if data were available (i.e. more than one species of predator) the only potential predator fish species with tracking in this study was Striped Bass. Misclassification of smolt movement patterns as Striped Bass (or any probabilistic weighting, with respect to the scaled estimate) can occur if an alternate predatory species consumed a tagged smolt and

presented movement patterns that more closely resembled those of Striped Bass. Misclassification due to alternate predators is most likely limited to that of piscine predators as avian or terrestrial predators would be expected to remove the transmitter from the study area and would no longer be detected by receivers, as was the case for some tags in the study. In the event an acoustically tagged smolt is consumed by a predator and few to no subsequent detections are made on receivers, the model classification would be to a smolt under the binary classification scheme. This is primarily due to movement characteristic measurements (exception of average speed between detections) being greater for Striped Bass than smolts in addition to the number of variables (5) included in each tree of the forest.

To further address concerns with uncertainties in the smolt classifications we considered a three-level classification system where smolt movement patterns with assignment probabilities between 0.2 and 0.8 we classified as 'unknown' states. Based on subjective review of the detection histories, smolt tags identified as exhibiting bass patterns under this three-level classification system (i.e. ≥ 0.80 probability) should be regarded as at or approaching the minimal level of consumption. This is expected as the 'unknown' state likely captures those consumed tagged smolts in which bass expelled the tags before the model could adequately respond to the behavioural change (i.e. model response time) in addition to possible intermediate smolt/bass movement behaviours (e.g. alternate piscine predators). One half of the estimated striped bass predation from three-level classification scheme, agreed perfectly with the binary classification scheme. This is indicative of the level of agreement between trees within the RF model. The percent of 'unknown' tag classifications was generally greater for NW smolt tags compared to the SW smolt tags (exception 2016). Given the higher degree of spatial and temporal overlap for Striped Bass and NW smolts, model response time to predation events may account for the greater percent of unknown classifications. To summarize, several factors can affect the probabilistic assignment of the movement patterns of individual fish: the fish was not consumed by a predator but

displayed a high level of in-river movement variability inconsistent with smolt or bass movement patterns; the tagged fish was consumed by a Striped Bass but there was an insufficient number of post-predation detections for the model to assign the movement pattern with a reasonable degree of certainty; the tagged smolt was consumed by an alternate predator with intermediate movement characteristics between smolts and bass; the tagged smolt died in the estuary for reasons other than predation after having moved or been displaced by currents before dropping out of the detection range of receivers; the tag was expelled by the smolt in the estuary.

Advances to address this question could be made using technologies that can define when and where consumption events occur. One such technology is predator tags which can signal consumption events based on a change in identification code triggered by the change in pH associated with the predator's gastrointestinal tract (Halfyard et al. 2017). This technology could define predation events more precisely than from movement pattern data as used in this study. Despite the ability of this technology to highlight consumption events at finer temporal and (potentially) spatial scales they are still not capable of fully defining when and/or where the predation event occurred because the triggering of the change in tag signal is subject to a time lag associated with consumption, digestion of the prey, and the switch in the identification code which would signal the consumption event.

Despite the method of interpreting the inferred percentage of smolts consumed by Striped Bass, the NW smolts were inferred to have been subjected to a greater than two-fold consumption rate in three of four years (exception 2013) relative to smolts from the SW. In addition, all three methods of interpretation display similar annual trends in consumption percentages. Note however that for the 2015 study year, the estimated Striped Bass spawner abundance in the Northwest Miramichi was the second highest of the assessed time series (301,000 spawners; DFO 2017), but the percentages of inferred tagged smolts consumed by Striped Bass was the lowest estimate for both stocks. This suggests that factors beyond Striped Bass abundance, such as spatial and temporal overlap of the two species in

the estuary, may be important in defining smolt predation rates by Striped Bass. The timing of smolt migrations and the location and timing of Striped Bass spawners on the staging and spawning grounds are both largely conditioned on, but not limited to, similar temperature ranges (Chaput et al. 2002; Douglas et al. 2009). Future research should focus on factors capable of predicting the degree of spatial and temporal overlap between Striped Bass and both NW and SW Miramichi salmon smolts and how this may be affected by variations in environmental conditions.

The greater the spatial and temporal overlap between predator and prey the more likely a predation event is to occur (Hebblewhite et al. 2005). Spatial and temporal overlap of the two species varied by year and stock in the Miramichi estuary. The variation of between stock spatial and temporal overlap is consistent with the negligible time spent by tagged Striped Bass in the SW Miramichi (Douglas et al. 2009). The estimated overlap between species occurred over a short duration, which is consistent with the one to two week period when most smolts migrate through that zone and to the brief window of time when Atlantic Salmon smolts were identified in Striped Bass stomach samples in the Miramichi (DFO 2016). The higher inferred percentages of predation on NW smolts are consistent with the higher estimated spatial and temporal overlap (2014 to 2016) between Striped Bass and salmon smolts in this area.

The highest potential for overlap between SW tagged smolts and tagged bass was in the main stem of the Miramichi and Miramichi Bay. The mainstem Miramichi estuary, below the confluence of the NW and SW is a staging area where pre-spawning Striped Bass aggregate before moving upstream onto the NW spawning grounds (Douglas et al. 2009; Douglas and Chaput 2011; DFO 2015). In 2015, most tagged Striped Bass moved upstream to the NW spawning grounds before the SW tagged smolts arrived at the main stem estuary (Fig. 6), and this corresponded with the lowest inferred consumption rate (1.9%) on SW tagged smolts during this study.

There is a growing and expressed concern by the public regarding the perceived negative consequences of a recovered and abundant Striped Bass population leading to a decline in abundance of wild Atlantic Salmon in the Miramichi River. Over the four years of this study, the percentage of tagged Atlantic Salmon smolts which were inferred to have been consumed by Striped Bass varied between 2% and 20%. It is not clear what impact Striped Bass predation on smolts has on adult return rates and/or population productivity as the vast majority of Atlantic Salmon smolts that migrate to sea do not survive to return as adults (ICES 2017). Return rates of Atlantic Salmon smolts to adults in monitored multi-sea-winter salmon populations of eastern Canada over the 2013 to 2015 smolt migration years ranged from 0.3% to 10% (ICES 2017). Including mortality estimates from this study suggests the majority of mortality seemingly still occurs beyond the estuary. It is also not known the extent to which the mortality incurred in estuaries is additive, although it is unlikely to be so, nor how representative the inferences based on tagged Atlantic Salmon smolts are of movement patterns, vulnerability to, and ultimately predation of untagged and unmanipulated Atlantic Salmon smolts (Adams et al. 1998; Anglea et al. 2004). Studies as reported here and the longer term experiments to estimate the relative migration success of tagged Atlantic Salmon smolts in the Miramichi River and in neighbouring rivers without spawning Striped Bass populations (Chaput, G., Daniels, J., Carr, J., Jonsen, I., and Whoriskey, F. In review) provide important information with which to address questions of predator/prey interactions of species of joint interest and to support management interventions. The question of whether increased Striped Bass abundance with associated biologically significant predation rates on migrating salmon smolts is the cause of reduced abundance of anadromous Atlantic Salmon in the Miramichi may best be answered by undertaking a large scale ecological experiment to reduce the abundance of Striped Bass in the Miramichi River over a number of years and to quantify metrics of responses such as consumption rates of tagged Atlantic Salmon smolts and the changes in abundance of adult wild Atlantic Salmon. While it is generally considered that the majority of Atlantic Salmon mortality is occurring at sea, managing any

449 impact occurring within the river/estuary is far easier to address from the perspective of, but not limited
450 to, management resources and capabilities.

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567 *Table 1. Summary of smolts tagged by stock and by year. Model output is based on the number of smolts*
568 *with detections in the study site. Model output is presented as the percent of smolts movement patterns*
569 *classified as Striped Bass patterns (i.e. consumed) under the binary classification criterion, as the scaled*
570 *estimate and estimated with ≥ 0.80 probability of belonging to the bass movement patterns.*
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Year	Miramichi River stock	No. released	Fork length (cm)	No. smolts with ≥ 1 detections in Miramichi estuary	No. smolts with ≥ 1 detections at Strait of Belle Isle	Inferred % of tagged smolts exhibiting Striped Bass movement patterns		
			Mean (range)	binary scaled ≥ P(0.80)				
2013	Northwest	40	14.0 (12.6,16.7)	36	2	16.7	19.4	13.9
	Southwest	65	14.6 (13.4,16.7)	41	5	17.1	16.5	14.6
2014	Northwest	50	13.6 (12.1,16.7)	40	5	17.5	19.9	17.5
	Southwest	80	14.2 (13.2,16.9)	50	7	8.0	9.0	8.0
2015	Northwest	80	14.2 (13.3,17.7)	70	17	6.7	9.2	6.7
	Southwest	80	14.2 (13.0,17.0)	59	11	1.9	2.6	1.9
2016	Northwest	60	14.1 (12.9,18.2)	50	8	18.0	17.6	16.0
	Southwest	59	14.0 (12.9,15.9)	28	8	7.1	8.2	3.6

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573 *Figure 1. Map of the Miramichi River in New Brunswick, Canada. Receiver locations (black outlined*
574 *circles) are denoted by their respective distance (km) up river with the zero km mark defined as the*
575 *receiver array located at Miramichi Bay mouth. Smolt release locations (black outlined star) are located*
576 *in both the Southwest and Northwest Miramichi Rivers. Inset map depicts the Gulf of St. Lawrence as*
577 *well as receiver arrays (black outlined solid line) that span the two entrances/exits of the gulf, the Strait*
578 *of Belle Isle (SoBI) array and the Cabot Strait (Cabot) array.*
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Figure 2. Examples of movement tracks of tagged Striped Bass and Atlantic Salmon smolts with estimated probability of membership to the bass-like classification in the Miramichi estuary. Panels a through d represent movement patterns of an assumed ‘true’ smolt given its detection at the Strait of Belle Isle (SoBI). Panel b represents an individual with an ‘atypical’ movement track of a smolt that was detected at SoBI. Panel e represents typical detection pattern of Striped Bass (assumed to represent true bass movement). Panel f shows a smolt movement pattern with an estimated assignment probability of 0.99 of being a Striped Bass pattern. Under the binary classification the detection history of the transmitters associated with panel g and h suggests membership to the smolt behaviour and bass behaviour classification respectively, however there is uncertainty as to which class (smolt vs. bass) they belong to. Horizontal grey shading represents the location of defined Striped Bass spawning grounds.

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Figure 3. Bivariate plot of quantified movement characteristics. From left to right: Number of days of detections (DiS), Number of days of detections in defined striped bass spawning ground (DoSG), Tally of the number of upstream or downstream directional changes (NoR), The cumulative upstream distance travelled in kilometers (UpStDist), Count of days between first and last detection on defined striped bass spawning ground (TRoSG), The average speed (km day⁻¹) between detections (AvgSpd), the total distance travelled between detections (TotDist), and the number of visits and switches between the Northwest and Southwest branches of the Miramichi River (RivSwi). Upper panel reflects relationship between movement characteristics and the lower panel presents the respective correlation. Colored circles are smolts (white) and Striped Bass (black) from the training data set.

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Figure 4. Frequency distribution of probabilities for all smolts with Striped Bass movement patterns. Each bar of the histogram represents 10 percent bins, for each smolt stock tagged, between 0.00 and 1.00 probability of Striped Bass movement characteristics. The vertical line at 0.50 represents the cut-off point at which the model separates classifications under the binary scheme. Dashed vertical lines at 0.20 and 0.80 represent the arbitrary cut-off, with probabilities ≤ 0.2 classified as smolt movement patterns, probabilities ≥ 0.8 classified as bass movement patterns and unknown movement patterns between 0.20 and 0.80.

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617 *Figure 5. Proportion of smolt detection patterns classified as bass-like with probability ≥ 0.80 (black) and*
618 *classified as unknown with probabilities > 0.20 and < 0.80 (grey) for each smolt stock. Corresponding*
619 *values are shown above each stacked bar.*
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623 *Figure 6. Two dimension (geographic location, date) plots and associated density isopleths of tagged*
624 *Striped Bass and tagged Atlantic Salmon smolts in the Miramichi estuary. Each point represents the*
625 *mean daily upstream position (MDUP) for each transmitter. Smolts used to calculate densities were only*
626 *those predicted not to have Striped Bass movement patterns under the binary classification scheme.*
627 *Upper panel (a) MDUP is calculated using detections on Northwest and mainstem Miramichi River*
628 *receivers, whereas, lower panel (b) MDUP is derived from Southwest and mainstem Miramichi River*
629 *receivers. Furthermore, MDUP is estimated for Striped Bass, Northwest Miramichi smolts (a) and*
630 *Southwest Miramichi smolts (b) by year. The horizontal line at $y=46$ represents the confluence of the*
631 *Northwest and Southwest Miramichi Rivers with the mainstem river. Contours for estimated 2D*
632 *utilization distributions via kernel density estimation overlay MDUP for each panel and sub-panel. The*
633 *outermost contour represents the 95th isopleth. For each Atlantic Salmon smolt stock estimates of*
634 *percent of the area of the 2D density overlapping the corresponding bass 2D density area is in the upper*
635 *right corner of each smolt stock's sub-panel. Black triangles reflect release dates of smolts for respective*
636 *smolt stocks and years.*
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