Determining early marine survival and predation by endothermic predators on acoustically tagged Atlantic salmon (*Salmo salar*) post-smolts

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Abstract

Many Atlantic salmon (*Salmo salar*) populations have experienced significant declines for decades throughout North America and Europe. Mortality due to marine mammal predation during their early marine life could be an important factor contributing to these declines and limiting their population recoveries. However, quantifying predation events, and particularly the extent of marine mammal predation on Atlantic salmon, remains a challenge. In this study, we estimated the contribution of mesothermic and endothermic species predation to the mortality of Atlantic salmon post-smolts during their early marine life using acoustic telemetry. Predation events were inferred from changes in temperatures and depths experienced by acoustically tagged hatchery-reared Atlantic salmon smolts. No salmon were consumed by mesothermic predators, with most endothermic predation events being classified as marine mammals. Post-smolt mortality during the study period was low overall in both years (13.1%–16.7%), with endothermic predation accounting for 33.1%–42.9% of all marine mortality events (5.2%–5.6% mortality). Our results suggest that the current low return of adult Atlantic salmon observed in this area in recent years was not heavily influenced by endothermic predation on post-smolts in the first weeks at sea.

Key words: telemetry, mortality, migration, pinnipeds, birds

Introduction

Historically, Atlantic salmon (*Salmo salar*) were present in thousands of rivers throughout eastern North America and Europe, although relatively few stable spawning populations remain (Jessop 1975; Lennox et al. 2021; Thorstad et al. 2021). Significant declines have occurred in Atlantic salmon populations in recent decades, with several subpopulations now listed as threatened or endangered, particularly at the southern limit of their geographic distribution (National Research Council (NRC) 2004; Chaput 2012). While Atlantic salmon face many stressors throughout their life history (Cairns 2001; Forseth et al. 2017; Dadswell et al. 2022), a widespread and persistent decline of Atlantic salmon continues, despite drastically curtailing retention fisheries and investment in freshwater habitat restoration. This suggests that factors related to at-sea survival are likely responsible for constraining salmon abundances and population recoveries (Chaput 2012; ICES 2017, 2020; Olmos et al. 2019).

For Atlantic salmon, most marine mortality is thought to occur primarily during the early marine phase (Thorstad et al. 2012b), though mortality during the second year at sea could also be important for multi-sea-winter fish (Chaput 2012). In some cases, significant mortality occurs during smolt downstream migration (Flávio et al. 2020). While estuarine and early marine mortality of Atlantic salmon post-smolts has been determined in numerous studies using acoustic telemetry (see summary from Thorstad et al. 2012b; Gibson et al. 2015; Hawkes et al. 2017; Vollset et al. 2017; Daniels et al. 2018; Lothian et al. 2018; Halttunen et al. 2018; Chaput et al. 2019; Flávio et al. 2020), elucidating the cause or causes of this mortality has been challenging. Identifying the causes of early marine mortality is necessary to determine when and where actions, if any, can most effectively be undertaken to foster population recovery.

Predation has been identified as an important source of mortality for Atlantic salmon post-smolts during their estuarine and early marine life (Falkegård et al. 2023). For ex-

ample, Gibson et al. (2015) identified predation on acoustically tagged Atlantic salmon post-smolts by striped bass (*Morone saxatilis*) when salmon movement patterns became more striped bass-like (i.e., consistent upstream movement and at relatively higher speeds). Predation on Atlantic salmon post-smolts by Atlantic cod (*Gadus morhua*) has also been detected through the use of tags with depth sensors that can identify atypical diving behaviour (Thorstad et al. 2011, 2012a). The combination of detection data with modelling and machine learning has also shown promise for more accurately assessing these mortality rates (Daniels et al. 2018; Notte et al. 2022). The impact of predation on post-smolts could be exacerbated when the abundance of prey species such as Atlantic herring (*Clupea harengus*) or lesser sandeel (*Ammodytes marinus*) is low (Svenning et al. 2005; Emmett and Sampson 2007). In Atlantic Canada, the abundance of pinnipeds—particularly grey seals (*Halichoerus grypus*)—has greatly increased during the recent period of Atlantic salmon declines, which could be a hitherto unquantified source of early marine predation of post-smolts (Rossi et al. 2021). There are also considerable populations of avian predators such as cormorants (*Phalacrocorax* spp.) and bald eagles (*Haliaeetus leucocephalus*), which are often observed feeding on fish in coastal areas of high marine productivity. Studies on both Pacific and Northwest Atlantic salmonids have recorded these avian species consuming migrating fish at significant rates (Dieperink et al. 2002; Evans et al. 2016; Flávio et al. 2021). Migrating Atlantic salmon post-smolts within Atlantic Canadian systems could be preyed upon by these species in a similar fashion.

Predation has been hypothesized to be particularly high in areas where salmon are reared in large-scale commercial sea cages (Amiro 1998; Cairns 2001; Butler and Watt 2003). As salmon aquaculture sites are often located along the migratory corridors of Atlantic salmon post-smolts (Ford and Myers 2008) and attract marine mammals such as pinnipeds (Heredia-Azuaje et al. 2022), the presence of open-net pens could enhance marine mammal predation on post-smolts (Amiro 1998; Cairns 2001; Butler and Watt 2003). Escapees of farmed fish from aquaculture sites have been linked to a potential pinniped learning behaviour (Amiro 1998; Cairns 2001). That is, the regular occurrence of escaped farmed salmon in the ocean could lead pinnipeds to recognize salmon as a regular prey option, thereby impacting the incidence of marine mammal predation on co-occurring wild salmon and their marine survival rates (Amiro 1998; Cairns 2001). Predators attracted to sea cages have thus been identified as a marine threat that may limit the recovery of endangered or threatened wild Atlantic salmon populations (DFO 2010).

However, direct evidence of marine mammal or avian predation on Atlantic salmon post-smolts is presently lacking in areas with and without salmon aquaculture (Amiro 1998; Cairns 2001). Lacroix et al. (2004) reported losses of post-smolts near aquaculture sites where potential predators had been frequently observed, though they could not directly attribute post-smolt mortality to predation. Hamoutene et al. (2018) recently reported high mortality rates of farmed salmon released from salmon aquaculture sites located in Fortune Bay and suggested that predation on salmon could be high in this area. Likewise, telemetry work on juvenile Pacific salmon species found a high incidence of mortality during migration past salmon aquaculture sites, which was largely assumed to be due to pinniped predation, owing to their high abundance in the area and the known attraction of pinnipeds to farm sites (Clark et al. 2016; Rechisky et al. 2019; Moore and Berejikian 2022). Hence, there is a need to understand the magnitude of the mortality caused by marine mammals and seabirds on post-smolts in areas where they co-occur with sea cages.

Acoustic telemetry has been used to determine predation occurrence and levels in Atlantic salmon post-smolts (Lennox et al. 2023). As the technology has matured, transmitters have been paired with ancillary sensors to measure parameters such as pressure (i.e., swimming depth), temperature, acceleration, and digestion that can all provide further insight into the occurrence and potential cause of mortalities (Crossin et al. 2017). The sensors can highlight uncharacteristic behaviour changes of tagged individuals, such as a surface-oriented species performing deep dives, a body temperature increase from ambient to elevated temperature (ectothermic transition to mesothermic or endothermic), changes in swim or burst speed, or by direct measure of predation by the digestion of a polymer film on the tag while it is in the acid of a predator's stomach changing the tag signal (predation tag, see Halfyard et al. 2017), any of which provides further lines of evidence to recognize mortalities (Klinard and Matley 2020). Similar analysis of fine-scale data stored on another type of electronic tag suitable for large (>50 cm length) fishes (satellite tags) allowed investigators to distinguish predation events by ectothermic, mesothermic, and endothermic species by recorded tag temperature increases from ambient to ~20 or 37 °C, but not necessarily between different marine mammal species based on dive patterns recorded by depth sensors (Lacroix 2014; Seitz et al. 2019; Strøm et al. 2019). However, the application of data from depth and temperature sensors in acoustic transmitters to quantify endothermic predation on post-smolts has thus far been rare. Acoustic tags now come in sizes sufficiently small to allow for application on small fish, such as salmon smolts, which presents a novel method to empirically quantify marine mammal and avian predation.

The objective of this study was to determine the proportion of migrating Atlantic salmon post-smolts that were preyed upon by endothermic (e.g., marine mammals, birds) and mesothermic (e.g., sharks, tuna) predators using acoustic telemetry in a region with a high concentration of active sea cages. Through the analysis of sensor temperature and depth data, we quantified the prevalence of known predation as a proportion of overall mortality to determine its significance to salmon survival during the early marine phase.

Methods

Study site

The study was conducted in Passamaquoddy Bay, a sub-basin of the Outer Bay of Fundy (BoF), which straddles the New Brunswick (Canada)—Maine (United States) border. The

work occurred between May–July 2019 and May–November 2021 (Fig. 1). The Passamaquoddy Bay is a semi-enclosed system subjected to extreme tides (~8 m during spring tides) and receives considerable freshwater input from the St. Croix and Magaguadavic Rivers (Bailey 1957). The inner basin of Passamaquoddy Bay is sheltered from the BoF by several islands and shoals. Deer Island is the largest of these islands, which, along with the other Fundy Isles (Campobello Island and several smaller islands), blocks the mouth of Passamaquoddy Bay from the BoF, aside from two main exit passages (Western and Big L'Etete passages) and two minor exit passages (Doyle's and Little L'Etete passages; Fig. 1). The extreme tidal action of the region, in tandem with complex bathymetry and narrow passages between several islands and shoals, creates considerable upwelling of deep, cold water from the BoF and significant currents. Tidal currents are strong at exit passages, with Big L'Etete Passage experiencing currents of up to 2 m s^{-1} (Bumpus et al. 1959). These conditions provide opportunities for both marine life and industry (i.e., aquaculture, fishing), with several species of shorebirds, large marine predators, and schools of pelagic species such as Atlantic mackerel (*Scomber scombrus*) and Atlantic herring frequenting Passamaquoddy Bay and its neighbouring areas of Cobscook Bay and Back Bay throughout the spring, summer, and autumn.

The high water turnover rate (1–2 days in the outer bay, 7 or more days in the inner basin) combined with the low water temperature makes this area suitable for rearing Atlantic salmon in sea cages (Brooks 2004). There are over 90 salmon aquaculture lease sites in Southwestern New Brunswick (Chang et al. 2014), though less than half of these are active at any time (see Fig. 1 for active lease sites at the time of the study). Passamaquoddy Bay and the surrounding areas where Atlantic salmon aquaculture is prevalent are divided into Bay management areas (BMAs). Each BMA is on a 3-year cycle (fallow, introduction, and grow-out) to ensure that single cohorts of farmed salmon are raised in any given BMA and to reduce the spread of diseases such as infectious salmon anemia (Chang et al. 2014). The study area is comprised of three BMAs—BMA 1, BMA 2a, and BMA 3c—which are offset from one another by 1 year (i.e., when BMA 1 is in the final grow-out stage and BMA 2a is introducing hatchery post-smolts, BMA 3c is fallowed). BMA 1 covers the majority of aquaculture lease sites in the bay, particularly those within the expected migration routes of salmon smolts that leave the Magaguadavic River. These farms were all in the grow-out and introduction stages of the 3-year cycle in 2019 and 2021, respectively.

The high level of productivity caused by extreme tides, currents, and the upwelling of deeper, nutrient-rich water into shallower areas make Passamaquoddy Bay and surrounding areas a hotspot for marine mammal activity. Several mesothermic and endothermic predatory species reside in the area year-round or seasonally, including harbour seal (*Phoca vitulina*), grey seal, harbour porpoise (*Phocoena phocoena*), sharks, tuna, several species of seabirds, and a few species of baleen whales. The presence of salmon farms may attract higher numbers of individuals than would be normally expected for these predators in the area (Nelson et al. 2006). Both harbour and grey seals are known to frequent active salmon farm sites throughout Passamaquoddy Bay and surrounding regions, evident through the high use of anti-predator nets and deterrents (Jacobs and Terhune 2002). While the large number of harbour porpoise sightings during the summer months indicates a significant population of these cetaceans within the bay, their distribution is not as easily characterized as grey and harbour seals that can be assessed at rookeries and haul-out sites (Fig. 1). The majority of seal haul-out sites are scattered throughout the Fundy Isles and Head Harbour Passage, with some only used during low tide. A smaller number of haul-outs exist within the inner basin, and there are accounts of seals travelling into both the St. Croix and Magaguadavic River estuaries.

The St. Croix and Magaguadavic rivers both supply large amounts of freshwater to the Passamaquoddy Bay system and provide key habitat for estuarine species. They were historically significant producers of wild Atlantic salmon (Carr et al. 1997; Jones et al. 2010). However, adult returns have declined precipitously in the St. Croix River since industrialization (e.g., pulp mills, hydroelectric dams) and are nearly extirpated in that system, with near-zero adult returns from non-hatchery salmon for over a decade (Jones et al. 2010). Substantial declines have also occurred in the Magaguadavic River during the last two decades, with less than ten adult Atlantic salmon returning to spawn each year in the last 10 years (Jones et al. 2010; Atlantic Salmon Federation 2019). The Magaguadavic River was chosen herein as the study system given the higher (albeit minute) wild Atlantic salmon population, logistical constraints (e.g., site access and ability to provide sufficient coverage with small numbers of acoustic receivers), and comparability to previous work that showed a more complex migration pattern for post-smolts leaving the Magaguadavic River estuary than observed in the St. Croix River (Lacroix et al. 2004). The river flows southeasterly over 97 km before emptying into Passamaquoddy Bay. An operational hydro-electric dam (13.4 m height) and its downstream fish bypass are located at the head-of-tide in the town of St. George, with a fishway that facilitates upstream migration of anadromous species around the dam in the same area (Martin 1984). Post-smolt migration timing and pathways out of the river may take different forms, given the complexity of the bay and interactions with potential risks such as aquaculture sites, farmed salmon escapees in the marine and estuarine environments, and marine mammal or seabird hot-spots (e.g., upwelling, seal haul-outs, and nesting sites). Previous telemetry work conducted in the area has shown that post-smolts released from the Magaguadavic River may take diverse paths to reach the BoF, but most seem to travel through the Western and Head Harbour passages (Lacroix et al. 2004; Quinn et al. 2022; Fig. 1c), where there is a high possibility of interacting with aquaculture operations and marine predators such as seabirds, mesothermic fish, seals, and porpoises.

Acoustic array

The acoustic receiver network consisted of numerous instruments placed throughout the Passamaquoddy Bay region and the wider BoF in southwestern New Brunswick ($n = 129$ in 2019, $n = 197$ in 2021; Figs. 1a and 1b). Deployments were

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Fig. 1. Map of Passamaquoddy Bay and associated acoustic receivers deployed in (*a*) 2019 (*n* = 129) and (*b*) 2021 (*n* = 197), including (*c*) known seal haul-out sites, salmon farm lease sites, Bay management areas (BMAs), and generalized migratory paths of Atlantic salmon smolts leaving the Magaguadavic River estuary, based on results from Quinn et al. (2022). Receivers placed at aquaculture sites are displayed as red dots; all other receivers are black dots. Dots with a white "X" in the centre denote receivers that were lost during the study period. The blue and green stars indicate the above- and below-dam release sites for the smolts, respectively. Key areas of the study site include the inner basin of Passamaquoddy Bay (PB), St. Croix River (SCR), Magaguadavic River Estuary (MRE), Western Passage (WP), Doyle's Passage (DP), Little L'Etete Passage (LLP), Big L'Etete Passage (BLP), Cobscook Bay (CB), Lubec Narrows (LN), Head Harbour Passage (HHP), Quoddy Narrows (QN), and Fundy Isles (FI), as well as the two main islands: Campobello Island (CI) and Deer Island (DI). All layers are projected in NAD83/UTM.
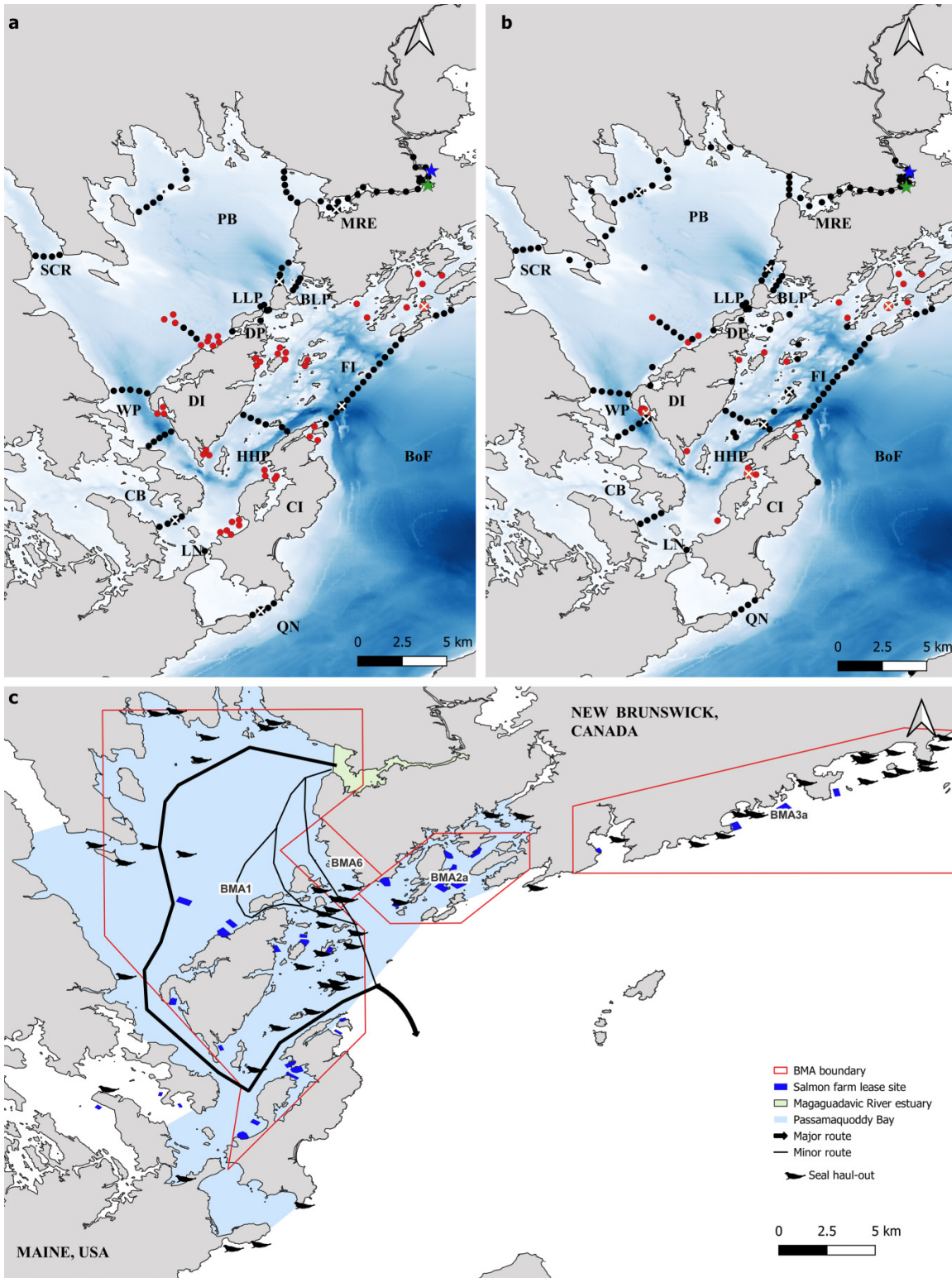
conducted prior to tagging smolts between April and May of each year, and consisted of VR2W, VR2Tx, and VR2AR receiver models (Innovasea Systems Inc.; Halifax, NS, Canada) that operated at 69 kHz. Generally, VR2W and VR2Tx units were attached to a rebar cage on 150 lb blocks and accessed by line and surface float. VR2AR units—reserved for locations of high traffic, great current, or depth, such as passageways—were likewise mounted to a 150 lb concrete block with a 2 m float line and sub-surface floats to provide lift and facilitate recovery.

In the Magaguadavic River, receivers were deployed in strategic locations from the site of tagged smolt release and then continued downstream through the estuary (~7 km long, average of ~300 m wide). Receiver arrays were also placed at the mouths of each of the main estuaries in Passamaquoddy Bay—the Magaguadavic and St. Croix rivers (Fig. 1). In the marine environment, twin receiver arrays were placed across exit passageways to assess the directions of movement of tagged fish through the passageways on the north and south side of Passamaquoddy Bay. A single array was placed across Cobscook Bay as modelling work suggested that post-smolts may travel into this area before ultimately migrating out through the Head Harbour Passage and the terminal arrays for the study, the Fundy Isles or Quoddy Narrows (Fig. 1; Quinn et al. 2022). Several individual receivers were deployed at 20–24 salmon aquaculture sites and selected seal haul-out sites to help monitor salmon behaviour as they migrated out of the bay. Although post-smolts generally left the receiver network within several weeks of release, telemetry data continued to be collected between May–July 2019 and May–November 2021.

Due to the noisy acoustic environment in the BoF—caused by strong tidal and surface currents and, at times, heavy vessel traffic—receiver range and detection efficiency were sometimes limited (see supplemental information for environmental noise and detection efficiency data, Table S1). Additionally, several receivers were unrecoverable at the end of the study period in both years, leading to gaps in coverage ($n = 7$ in 2019, $n = 6$ in 2021; Figs. 1a and 1b); however, movement patterns for individual fish could generally be reconstructed with neighbouring receivers or arrays. Upon receiver retrieval, detection data were downloaded for initial inspection in VUE (v. 2.7.0; Innovasea Systems Inc.; Halifax, NS, Canada) and to apply time corrections to instrument clock drift. Raw detection files were collated by year, and fish movement patterns were analyzed separately.

Fish collection and surgical procedures

Due to the low abundance of wild Atlantic salmon in this area, we opted to tag hatchery-reared smolts (mean FL/weight = 150.1 mm/34.1 g and 192.7 mm/73.1 g in 2019 and 2021, respectively; Table 1) from a cultured strain originating from a nearby system (the Tobique River). Genetically, these hatchery fish are within the same salmon genetic lineage as outer BoF salmon (Verspoor 2005). The migration, residence time, size range, and early marine survival of these fish were similar to those of wild Atlantic salmon post-smolts from the Magaguadavic River (Lacroix et al. 2004; Quinn et al.

2022), and as such, they were considered a suitable surrogate for wild smolts in this area.

Surgical implantation of acoustic transmitters (V7TP-4x; 7 × 23 mm; 1.0 g in water; InnovaSea Systems Inc., Halifax, NS, Canada) was performed on 160 and 150 hatchery-reared smolts at the Mactaquac Biodiversity Facility (MBF; Mactaquac, New Brunswick) in May to June 2019 and May 2021, respectively (Table 1). This equated to a tag burden of generally less than 2% of fish body weight. Smolts were individually anesthetized in a 100 mg L^{-1} tricaine methanesulfonate (MS-222; Syndel Canada, Nanaimo, BC, Canada) solution and remained in the bath until fully sedated (i.e., loss of equilibrium, shallow ventilation, and no righting reflex). Fish were moved to a padded V-trough with gills irrigated by a low dose (50 mg L^{-1}) of MS-222 administered through a recirculating pump. A 15 mm incision was made along the ventral midline, followed by the insertion of a transmitter into the peritoneal cavity, and then two interrupted sutures were used to close the incision (4–0 PGA Vicryl, FS-2 cutting, 3/8″; Ethicon, Raritan, NJ, USA). The smolts were held in a 3000 L rectangular tank for 2 days before transport from MBF to assess for any tagging-related moribundity or behavioural changes. For the rare individuals that were moribund or experienced tag rejection, the transmitters were replaced in naïve fish on the day of transport ($n = 7$ in 2019 and $n = 2$ in 2021). Tags were tested again at release to ensure that they were active.

Acoustic transmitters were activated for 10 min presurgery to ensure all tags were operational, then entered a two-day dormancy over the post-surgery recovery period to conserve battery life. At the time of fish release, tags were set to a high-power, short-interval transmission (mean of 30 s, range 20–40 s) for 20 days, then at a low-power, long-interval transmission (mean of 90 s, range 60–120 s) until the battery expired (estimated 72 days). This programming was intended to increase the potential for detections in the noisy coastal environment as well as to conserve battery life for potential detection at more distant acoustic arrays (e.g., Ocean Tracking Network [OTN] Halifax Line, Cabot Strait Line). The drawback of this approach is that it can lead to a large number of tag collisions at the release site. As a result, some fish may have been missed by some of the receivers near the release sites. Tag collisions were expected to diminish as post-smolts migrated out of the Magaguadavic River and eventually not be an issue as the fish dispersed from the release sites to the ocean.

Additionally, transmitters were equipped with temperature (−5 to 35 °C range; 0.5 °C accuracy; 0.15 °C resolution) and pressure (0–204 m range; ±1.0 m accuracy; 0.9 m resolution) ancillary sensors that alternated in the transmission of observed values. These data were used to delineate fine-scale changes in behaviour that were indicative of predation events in the tagged fish. The transmitters were sensitive enough to differentiate the expected ambient temperatures of tags in potential mesothermic (i.e., shark, tuna) predators from those consumed by endothermic (i.e., marine mammal, bird) predators. A rise in tag temperature occurs relatively rapidly after a tag is consumed; however, tag signals are only recorded when the tag is within the range of a receiver. While the internal temperatures of mammalian and avian species

Table 1. Lengths and weights of tagged Atlantic salmon smolts released into the Magaguadavic River in 2019 and 2021.

Release date	# of tagged fish	Average FL (mm)	Length std dev (mm)	Average weight (g)	Weight std dev (g)
24/5/2019	80	152.3	9.8	35.4	7.4
14/6/2019	80	147.9	6.3	32.8	3.9
	160				
14/5/2021	50	186.9*	14.3	68.8	14.9
21/5/2021	50	191.9*	16.0	71.4	16.9
27/5/2021	50	199.3*	12.6	79.0	13.1
	150				

*TL measurements converted to FL measurements using the following formula: FL (cm) = 0.916TL (cm) + 0.0402 (Jessop 1975).

differ (37 °C vs. 42 °C, respectively), with the temperature range capped at 35 °C, the temperature sensors are unfortunately not sufficient to discern avian and mammalian predators from each other. To do this requires a more careful examination of the displacement patterns of each tag. Tags in marine mammals were characterized by consistent transmissions through subsequent arrays, while those in avian predators were characterized as sporadic, disconnected detections, often bypassing multiple arrays between detections. We interpret this as indicative of flying (i.e., multiple bypassed arrays between detections), assuming our arrays would not have inefficiencies at multiple locations for the migration of a post-smolt (or predator) to consistently go undetected.

Transport and release

Smolts were transferred by truck from MBF on the day of release—an approximately 1.5 h drive to the release site—in a 1000 L insulated container (Xactics, Cornwall, ON, Canada), with environmental conditions monitored and supplemental oxygen supplied. Prior to transport, a therapeutic dose of salt (2 PPT) was added to reduce stress and aid in the smoltification process.

Two release sites were chosen on the Magaguadavic River, consisting of an above-dam and a below-dam location. The above dam site was approximately 1.1 km upstream of the St. George Dam and in freshwater, while the below dam site was the head-of-tide in the Magaguadavic Basin (Fig. 1). In 2019, two release groups—on May 24th and June 14th—were used, with 40 fish released per site (40 fish × 2 locations × 2 groups = 160). In 2021, three release groups were used—on May 14th, 21st, and 27th—with 25 fish released per site (25 fish × 2 locations × 3 groups = 150). In all instances, fish were released in daylight and typically at low tide to minimize the contrast in salinity between the above and below dam release groups. Groups of approximately five fish were released in quick succession, with buckets carried from the truck bed container to the riverside. This release coincided with the local smolt run, which generally occurs between early May and early June of each year (Lacroix et al. 2004).

All animal care and surgical procedures were conducted under approval from the Fisheries and Oceans Canada (DFO) Regional Animal Care Committee (Animal Use Protocol # 19–21; 21–20) in conjunction with the guidelines and standards set by the Canadian Council on Animal Care (CCAC). A subsample of the population from which these fish were taken was screened for and found free of reportable disease prior to surgery and subsequent release. Releases were permitted through a DFO Introductions and Transfers Authorization.

Post-release monitoring and data analyses

All analyses were conducted in the R programming language (v. 4.1.3) using R Studio (v. 1.4.1717; R Core Team 2022). Smolt detections in the Magaguadavic River and estuary were separated from the Passamaquoddy Bay (i.e., marine) detections to better understand spatial, temporal, and habitat-associated factors that affected predator-induced mortality. Instances of riverine/estuarine and marine mortality were then determined through the presence of temperature anomalies (i.e., ≥20 °C) and uncharacteristic dive (i.e., ≥5 m) or migration patterns that would be indicative of a mammalian or avian predator. All post-smolts that were not successful at reaching the terminal arrays (i.e., Fundy Isles, Quoddy Narrows), but did not exhibit a temperature change, were considered to be an unknown mortality. Causes of these mortalities could include physiological stress, tagging injuries, ectothermic predators, or avian predation outside of detection range, among others. In particular, temperature sensor values were filtered to ≥20 °C; with temperatures between 20 and 35 °C due to mammals or bird predation and those plateauing near 20 °C (~10 °C above ambient temperature) indicating consumption by a mesothermic predator (i.e., shark, tuna). All records for transmitters exhibiting anomalous temperature values were examined in their entirety to determine if a predator was a mesothermic fish, a marine mammal, or a bird. Similar analyses were performed on tagged smolts that were undetected in the marine environment to check for predation in the estuary. While difficult to discern at times, avian predators were identified by sporadic and disconnected patterns (i.e., skipping multiple arrays between detections) in combination with a temperature of 35 °C, while marine mammals were identified by consistent detections at subsequent stations/arrays as they moved throughout the bay (in combination with a temperature anomaly). The most distant arrays in the receiver network, namely Fundy Isles and Quoddy Narrows, served as a final checkpoint for migrating post-smolts, with survival to this point assumed for any individuals last detected at either of these outermost arrays (unless indicated otherwise by a temperature sensor).

In this study, we estimated the survival of the post-smolts in the river/estuary and Passamaquoddy Bay habitats marked by detections at the Magaguadavic River terminal array and the two terminal arrays that represented the boundary of the study area, respectively (Fig. 1), using the "actel" R package (v. 1.2.1; Flávio and Baktoft 2021) via the "simpleCJS()" function. In acoustic telemetry, survival S_i between two arrays has traditionally been estimated using a simple Cormack–Jolly Seber (CJS) as (Perry et al. 2012):

$$(1) \qquad S_i = \frac{M_i}{M_{i-1}}$$

where M_i and M_{i-1} are the estimated number of fish that are alive at array i and $i-1$, respectively. As some fish may go undetected at either arrays due to a variety of reasons (e.g., tag collision, noise, and tilt), the number of fish alive at a given array is determined as:

$$(2) \qquad M_i = \frac{m_i}{p_i}$$

where m_i is the number of fish detected at array i and p_i is the detection probability at that array. The detection probability at array i can be estimated empirically using sentinel tags or using detections at subsequent arrays as:

$$(3) \qquad p_i = \frac{r_i}{r_i + z_i}$$

where r_i is the number of individuals detected at arrays i and $i + 1$, and z_i is the number of animals detected at array $i + 1$ but not at array i. The probability of detection at the terminal array is usually set to 1, as there are typically no other arrays beyond that can be used if any of the fish went through the terminal array undetected.

The implementation of the CJS model in the "actel" package study makes use of peer stations (in this case, neighbouring arrays or receivers) to determine survival by designated section, which in this case was either survival out of the estuary (Magaguadavic River terminal array) or survival out of the early-marine environment of Passamaquoddy Bay (Fundy Isle and Quoddy Narrows terminal lines, Fig. 1). The CJS model output from actel shows both detected individuals and estimated individuals at the terminal array of each section, based on forward efficiencies, which account for any missed detections at a particular array. For example, if a tagged individual was detected at station A upon release ("1"), not detected further down river at station B ("0"), but detected again by the subsequent station C ("1"), the coding of "101" would indicate to the actel package that this fish migrated past station B and should be considered present at station B, unless otherwise stated (i.e., if there is a way to bypass station B). In essence, this essentially inflates m_i in eq. 2 to M_i for the number of fish that were known to be missed at that array. For this study, only the estimated counts (using actual detections and peer stations) at each array are provided and are referred to as "estimated survival".

This package requires that all possible connections between subsequent stations be provided in a text file (includ-

ing stations with a one-way path, such as a dam). Due to the complex nature of this system and the multiple directions in which a post-smolt could travel once exiting the estuary, the Magaguadavic River terminal line had several peer stations that aided in estimated survival and provided an accurate estimation of post-smolts entering the early-marine environment, which was the primary focus of this study. Confidence intervals (CI; 95%) were calculated for CJS survival estimates using a bootstrap method via the R package "bootstrap". Estimated survival values used were the number of smolts released, the estimated successful migrants to the Magaguadavic River terminal array, and the estimated successful migrants to the BoF. Survival estimates were run through the package 100 000 times. Endothermic predation was also analyzed through correlation with smolt biometric data such as length and weight. All biometric entries had an additional column indicating predation or survival ("1" or "0", respectively). Biometric factors were entered into a generalized linear model in R, where both length and weight were considered independent variables of survival and the distribution was assumed to be binomial.

The CJS model helps incorporate detection efficiencies into the estimation, especially in our case where periods of high tidal currents or environmental noise could impact a receiver's detection range. Due to the reliance on subsequent stations for detection efficiencies, terminal arrays do not get assigned efficiency estimates through CJS. To overcome this, each terminal line consisted of multiple receivers, each of which had its own built-in transmitter. These transmitters are set to communicate with neighbouring stations in the array every 10 min. All station-to-station detections during the migrations were compiled and compared to the expected number of transmissions during that period (1 transmission every 10 min = 4320 per receiver every month). This proportion of actual and expected station-to-station detections allowed for an estimate of array efficiency.

Results

Overview

Of the 160 and 150 Atlantic salmon smolts that were tagged in 2019 and 2021, 96 and 107 were estimated (via CJS) to have reached the Passamaquoddy Bay, indicating a 60% and 71% (95% CI = 50.6%–69.4% and 64.7%–80.0%, respectively) riverine/estuarine survival, respectively (Table 2). All tagged smolts were detected in the Magaguadavic River and/or estuary at a minimum of one receiver downstream of their respective release site. Post-smolts that reached the terminal line of the Magaguadavic River estuary and entered Passamaquoddy Bay were generally ($n = 80$ in 2019, $n = 93$ in 2021) successful in migrating out of Passamaquoddy Bay (within the 20-day period where transmitter frequency was 20–40 s), with final detections at the outermost arrays (Table 2; see supplemental information for more detail). The terminal array efficiencies varied between year and location but were generally between 60% and 75%. Successful migrants remained within Passamaquoddy Bay (i.e., early marine environment) for 0.2–18.4 days (mean = 4.3 days) in 2019 and 1.4–13.5 days

Table 2. Survival and mortality estimates of tagged Atlantic salmon post-smolts during seaward migration through Passamaquoddy Bay.

Release date	Total	Disappeared in river/estuary	Migrated to Bay	Disappeared in Bay	Migrated to BoF
2019	160	64 [0]	96 (60%)	16 [5]	80 (83%)
May 24	80	23 [0]	57 (71%)	9 [2]	48 (84%)
June 14	80	41 [0]	49 (51%)	7 [3]	32 (82%)
2021	150	43 [0]	107 (71%)	14 [6]	93 (87%)
May 14	50	13 [0]	37 (74%)	4 [1]	33 (89%)
May 21	50	11 [0]	39 (78%)	6 [4]	33 (85%)
May 27	50	19 [0]	31 (62%)	4 [1]	27 (87%)

Note: Estimates for the estuarine migration are based on detections at the final estuary array as well as peer stations to account for any undetected fish. Migration to BoF relies solely on detections at the terminal array due to a lack of subsequent peer stations. Survival percentages during each stage of the migration and mortalities explained by endothermic predation (i.e., marine mammals, birds) are presented in parentheses and square brackets, respectively. Survival percentages for bay and BoF migration are cumulative and based on survivors from the estuarine environment.

(mean = 5.8 days) in 2021 before entering the BoF. Detections were recorded at each of the four passages, with 68%–71% and 17%–20% of post-smolts taking Western and Big L'Etete passages during outmigration, respectively (see Fig. 2). Over 90% of post-smolts exited through the Fundy Isle terminal array. The majority of individual migration paths were in proximity (1–3 km) to at least three farms, where interactions with marine predators could have been heightened (Figs. 1 and 2), with 69% and 54% of post-smolts being detected at farm receivers, respectively. However, it should be noted that in both years, approximately two-thirds of the post-smolts in this study, which focuses on early-marine survival, were from the below dam release group, indicating a higher riverine/estuarine mortality rate for the above dam treatment. The cause of riverine/estuarine mortalities was considered unknown; however, all tags were checked for temperature anomalies for evidence of consumption by mesothermic or endothermic predators, but no evidence for this was found. Aside from checking for endothermic predators, these observations in the river and estuary were not further analyzed, as the focus of this study was on survival in the marine environment.

In 2019, data from 16 tags indicated signs of mortality (i.e., did not make it to the terminal array or had temperature anomalies) in the early marine phase of post-smolt migration, representing a 16.7% mortality rate (95% CI = 9.4%–25.0%). Of these, five post-smolts had temperature and depth pattern anomalies indicative of an endothermic predation event (i.e., ≥20 °C, dives deeper than ≥5 m; Figs. S1–S4), which accounted for 31.3% of all observed marine mortalities (95% CI = 8.3%–55.6%) or 5.2% of post-smolts that left the estuary (95% CI = 1.0%–10.4%). Suspected predation events occurred within 4–7 days (mean = 5 days) post-release and were constrained to Western and Head Harbour passages (Fig. 3). There was no significant correlation between predation prevalence and the length (estimate = −0.0166; df = 159; z = −0.135; p = 0.893) or weight (estimate = −0.0061; df = 159; z = −0.034; p = 0.973) of released smolts.

In 2021, data from 14 tags showed signs of mortality in the early marine life of migrating post-smolts, representing a mortality rate of 13.1% (95% CI = 11.2%–27.1%). Of these, six individuals had temperature and depth pattern anoma-

Fig. 2. Paths taken by successfully migrated post-smolts as they exit Passamaquoddy Bay through one of four passages. Blue/green indicates fewer unique detections, while red indicates a high prevalence of unique detections. All layers are projected in NAD83/UTM.
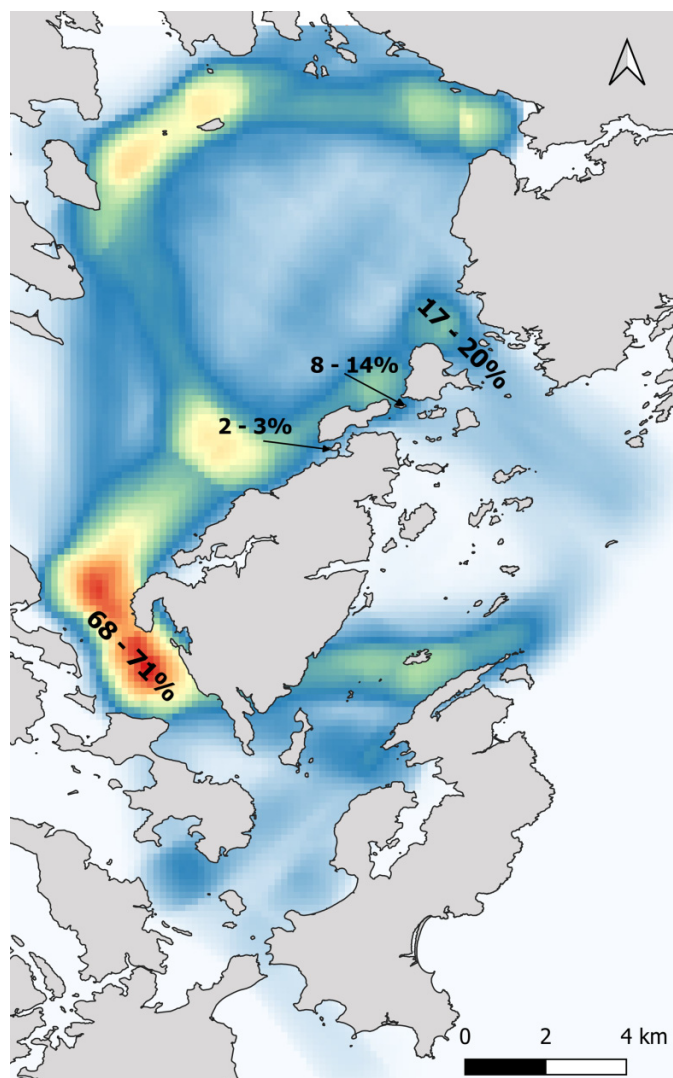
Fig. 3. Habitat boundaries (Magaguadavic River Estuary [MRE], Passamaquoddy Bay) used for CJS survival analysis and the nearest detections to endothermic predation events in both 2019 and 2021. Blue symbols indicate the "last alive" detections (temperature <20 °C) and red symbols indicate the "first consumed" detections (temperature >20 °C). All layers are projected in NAD83/UTM.
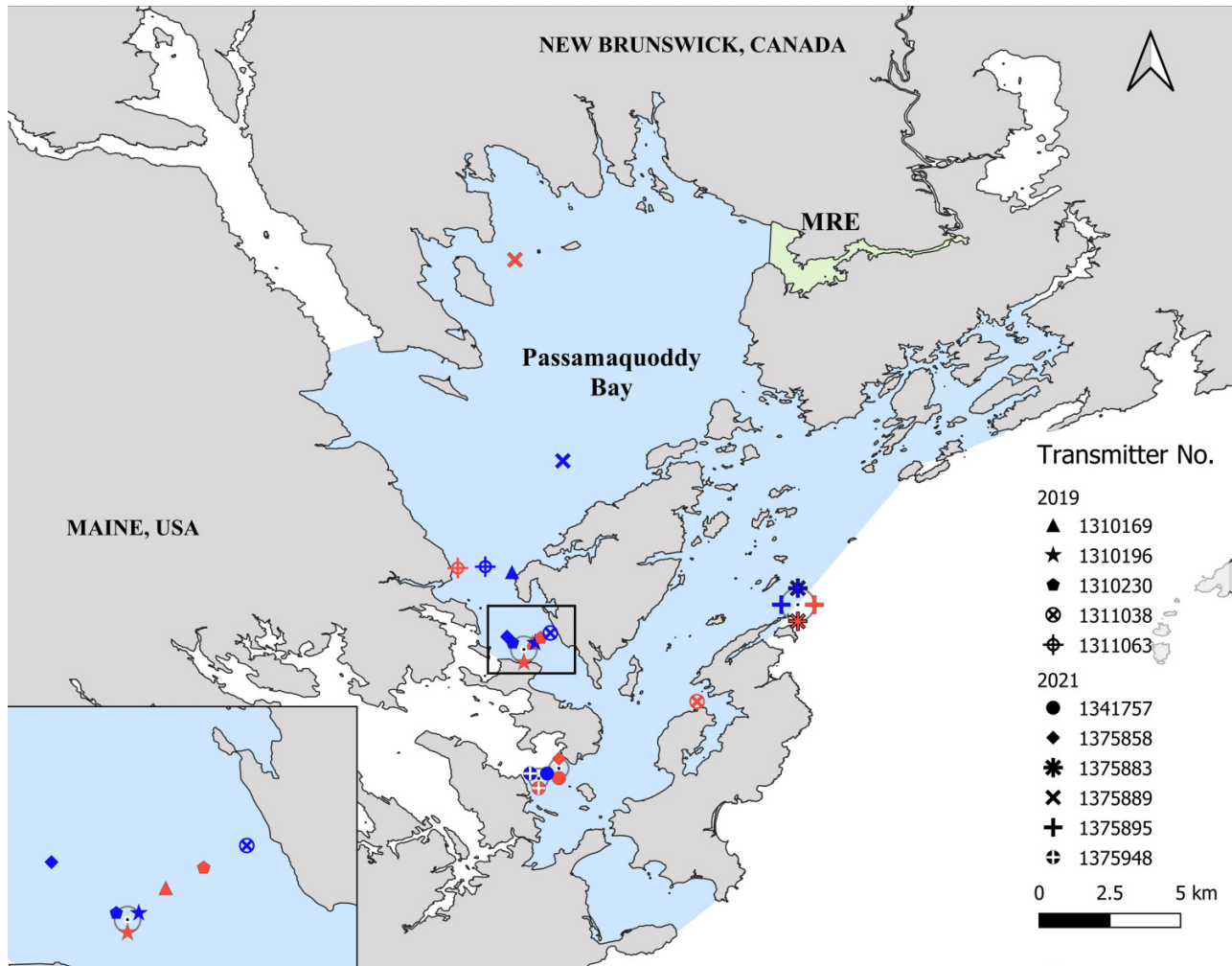
lies indicative of an endothermic predation event that accounted for 42.9% of all observed marine mortality (95% CI = 10.5%–52.2%), or 5.6% of post-smolts that left the estuary (95% CI = 1.9%–10.3%). Suspected predation events occurred within 3–12 days (mean = 7 days) post release, and were constrained to Cobscook Bay, the Fundy Isles, and the inner basin of Passamaquoddy Bay (Fig. 3). There was no significant correlation between predation prevalence and the length (estimate = −0.0346; df = 149; z = −0.340; p = 0.734) or weight (estimate = 0.0580; df = 149; z = 0.615; p = 0.538) of released smolts.

Identified predation events

Tag records for all endothermic predation events showed a sharp increase in temperature and were often correlated with a change in dive pattern that was uncharacteristic of post-smolt behaviour (see supplemental information for detailed dive patterns, Figs. S3 and S4). Where possible, these predation events were classified as marine mammal or avian predators based on movements throughout the bay (Table 3). None of the temperature anomalies had plateaued near 20 °C, ruling out any possibility of a mesothermic predator. In fact, most predation events relayed no transmissions between 20 and 35 °C. There were also an additional eight tags that showed instances of abnormal depth readings without a temperature increase. The time interval between the last "alive" and the first "consumed" detections for individual post-smolts that were confirmed as predated (i.e., ambient temperature to ≥20 °C) varied greatly among predation events, from as little as 4 min to over 6 h (Table 3). This made it difficult to accurately estimate predation time and location. In general, predation events could be narrowed down to a 1- to 2-h period during the night (20:00–06:00 AST), with no predation events observed between 10:00–16:00 AST. Collectively, the 11 transmitters that showed temperature anomalies in 2019 and 2021 stopped relaying data to receiver arrays within 48 h of predation, and in some instances, only a few detections were recorded after the predation event (Figs. S1–S4). Post-consumption dive patterns for tags believed to have been consumed by an endothermic predator varied in

Table 3. Metadata and endothermic predation event data of post-smolts released in the Magaguadavic River in 2019 and 2021.

Serial no.	FL (mm)	Weight (g)	Release date	Treatment	Last alive detection[b]	First consumed detection[b]	Predation event Δt (h:min:s)[c]	Time of predation[d]	Tidal phase	Likely predator[e]
1310169	155	36.0	24/5/2019	Below dam	WPI	WPO	1:54:11	Night	Flood	Mammal
1310196	150	32.0	24/5/2019	Above dam	WPO	WPO	1:36:21	Night	High	Mammal
1310230	146	32.6	14/6/2019	Below dam	WPO	WPO	1:38:12	Night	High	Mammal
1311038	139	28.9	14/6/2019	Below dam	WPO	MF-CI	2:11:39	Night	Flood	Mammal
1311063	154	36.8	14/6/2019	Below dam	WPI	WPI	1:49:07	Evening	High	Bird
1341757	200[a]	86.2	14/5/2021	Below dam	CB	CB	5:57:03	Evening/night	Low/flood	Mammal
1375858	212[a]	99.4	21/5/2021	Above dam	WPO	CB	6:20:36	Night/morning	Ebb/low	Mammal
1375883	190[a]	68.9	21/5/2021	Below dam	FI	FI	0:04:49	Night	Low	Mammal
1375889	181[a]	53.9	21/5/2021	Below dam	DI	MI	6:15:06	Night/morning	Flood/high	Bird
1375895	197[a]	77.0	21/5/2021	Below dam	FI	FI	1:43:58	Night	Ebb	Unknown
1375948	207[a]	92.6	27/5/2021	Below dam	CB	CB	5:23:13	Night/morning	Flood	Unknown

[a]TL measurements converted to FL measurements using the formula: FL(cm) = 0.916TL(cm) + 0.0402 (Jessop 1975).
[b]Locations of predation were Inner and Outer Western passage (WPI, WPO), Marine Farm near Campobello Island (MF-CI), Cobscook Bay (CB), Fundy Isles (FI), and inner Passamaquoddy Bay locations of Davidson's Inlet (DI), and Minister's Island (MI).
[c]Elapsed time between last alive and first consumed detections.
[d]Night = 20:00–06:00 AST; morning = 06:00–10:00 AST; evening = 16:00–20:00 AST.
[e]Based on movement and/or depth data, where applicable.

minimum dive depth, with some transmitters relaying repeated dives down to a minimum of 20 m with only brief intervals at the surface. For example, in combination with temperature readings above 37 °C, some transmitters in 2019 and 2021 relayed behaviours of suspected marine mammal predators, with multiple dives to minimum depths of 30–50 m and frequent surfacing, while another showed multiple dives of up to 60 m within a 20 min period (Tag IDs: 1310230, 1311038, 1375948, and 1341757; see supplemental information for more detail, Figs. S3 and S4). Temperature sensors allowed us to identify predation by endothermic predators, and some of the movement patterns gave relative confidence that these are likely marine mammal predators. However, the limitations of acoustic telemetry technology precluded the identification of marine mammal predators at the species level, as well as cases that could not be accurately determined as mammalian or avian predators.

Discussion

Our study highlights the utility of acoustic telemetry, in conjunction with ancillary sensors, to identify instances of mortality in Atlantic salmon post-smolts. Moreover, the data has allowed for the classification of suspected mortality events into a specific group of predators—namely endothermic predators (i.e., marine mammals or birds)—by interpretation of depth and temperature profiles. Overall, our study found that a total of 11 tagged post-smolts over the two release years showed clear signs of endothermic predation in the marine environment, with most cases believed to be attributed to pinnipeds based on movement patterns. There were no detections of temperature anomalies in the estuary. This may help to rule out marine mammal predation in the estuarine environment, but it is possible that several avian predation events could still have occurred. During the releases, there was an abundance of cormorants and other large

seabirds within the estuary (B. Wilson (personal observation, 2019, 2021)). Cormorant species have been recorded predating on salmonids, with one study showing a predation rate of 15.4% on adult brown trout (*Salmo trutta*) during their spawning migration (Källo et al. 2023). These individuals could have been flying over the bay after consuming salmon smolts and never landing within range of an array (prior to defecation of tag) to display the distinguishable, disconnected pattern coupled with an increased tag temperature of an avian predator. Similarly, it is possible that marine mammal predation occurring in the middle of Passamaquoddy Bay could be missed as well if these mammals never went through the receivers before defecating the tag. In both hypothetical cases, these smolts would be classified as an unknown mortality. However, even if all mortality observed (i.e., 10%–15%) was attributed to endothermic predators, it would not overly change the conclusions drawn from the results. Other potential causes of these unknown mortalities could be predation by ectothermic fish, interactions with anthropogenic disturbances (i.e., dams) or delayed surgery-related injuries, among others.

The mortality of Atlantic salmon post-smolts during their early marine life has frequently been determined using acoustic telemetry and is highly variable among studies, ranging from as low as 0% to 96% (Lacroix et al. 2005; Thorstad et al. 2007, 2011; Davidsen et al. 2009; Kocik et al. 2009; Chaput 2012; Daniels et al. 2019). However, these results are not always directly comparable, as the temporal scales (days to weeks) and spatial scales (<10 to >100 km) are highly variable among studies, and the causes of this mortality are usually unknown. In addition, the lack of ancillary sensors in most of these studies may lead to an overestimation of survival if a fish that was in the stomach of a predator was last detected on the terminal array (Klinard and Matley 2020). For instance, one of the post-smolts detected on the terminal array leading to the Bay of Fundy exhibited a temperature pro-

file characteristic of an endothermic predator in this study. Without this ancillary sensor, this fish would have been classified as a successful migrant, resulting in an overestimation of survival for that cohort. The magnitude of this bias is unknown in most studies involving acoustic telemetry (Klinard and Matley 2020).

In this study, the early marine mortality was overall low for Atlantic salmon post-smolts, averaging 10%–15% among years, and was comparable to values previously obtained in this area using acoustic tags without ancillary sensors (Lacroix et al. 2004; Quinn et al. 2022). Overall, endothermic predators consumed 5% of the post-smolts that successfully left the estuary and thus contributed to one-third of the early marine mortality. While previous research has shown that aquaculture sites can potentially attract marine mammals and other predators (Papastamatiou et al. 2010; Arechavala-Lopez et al. 2015; Callier et al. 2018), predation by endothermic predators on Atlantic salmon post-smolts was not centred around aquaculture sites in this study. This suggests that the predation risk of Atlantic salmon post-smolts by endothermic predators may be low around salmon aquaculture sites.

This mortality occurred over a short period of time (~4–5 days), creating a seemingly high annualized predation rate. It is important to realize, though, the minimal effect this predation would have on the recruitment of Atlantic salmon. Using an average 0.5% survival rate from smolt to returning adult for this area (Gibson 2004; Lacroix 2008; Gibson et al. 2015), the complete removal of endothermic predation events during this time would only amount to a survival rate of 0.53%. Even when factoring in the unknown mortality within the estuary and bay (some of which could be due to surgery stress), the return rate is still well below 1%. Therefore, other factors beyond early marine life may be of greater importance to the recruitment of Atlantic salmon in this region (Chaput 2012).

The ancillary sensor had a temperature cap at 35 °C, which made it possible to differentiate between tagged post-smolts and consumption by mesothermic or endothermic species. All predation events had a sharp temperature increase, which points to most predation events occurring outside the range of deployed receivers and that tag temperatures in predators' stomachs had stabilized at high temperatures by the time the predator moved within range of a receiver. One transmitter was able to record slight drops in stomach temperature, indicating additional foraging events after the post-smolt was consumed (Tag ID:1311038; Fig. S1). Differentiation between marine mammal and avian predation was difficult to distinguish without further examination of movement patterns. Sporadic, disconnected detections that skip multiple arrays or single-location detections are good indications that the endothermic predator could be avian, compared to consistent detections at subsequent gates being indicative of a marine mammal swimming through the study site. All predation events were determined to be from endothermic species, with the majority having a high likelihood of being marine mammals based on the observed movement patterns. However, predator E in 2019 and predators D and E in 2021 (Figs. S5 and S6) were detected multiple times before transmission ceased, but only on one receiver, which means

these predators could have been avian. Additionally, Predator B in 2021 only had one 35 °C detection at the Cobscook Bay array before transmissions ceased. Without confirmation of the movement pattern, it is not possible to determine with certainty that this was a marine mammal predation event and not an avian predator. Since birds and mammals often have different internal body temperatures, with birds having typically higher temperatures than mammals, an increase in the factory limit of the sensor to 40 °C could potentially resolve this issue for future studies.

Although useful as a secondary confirmation of predation, depth profiles were unable to provide details of species-specific dive patterns in this study due to the spacing between arrays. In fact, due to the patchy nature of acoustic data (e.g., maximum of one detection every 20–40 s, even for continuous detections), the sensor data only provides instantaneous readings. Therefore, depth readings only correspond to depth the animal was detected at, providing no information about the depth the animal was at for the majority of the time (even when the animal is within acoustic coverage). As such, the depth sensor provides a minimum dive depth. Dive duration could not be calculated due to the high probability a diving predator surfaced outside acoustic coverage (either in between transmissions or outside the detection range) before being detected at depth again. The three most common marine mammals in the area are harbour seal, grey seal, and harbour porpoise, which can all have similar-looking diving behaviour (Gjertz et al. 2001; Beck et al. 2003; Teilmann et al. 2007), especially when depth data are opportunistically collected, as is the case with acoustic receivers. Despite telemetry results being inconclusive for discriminating among these three species, the high density of pinnipeds within the main exit passages suggests that a portion of this predation could be caused by harbour and grey seals.

Similarly, predation by ectothermic fish was not easily distinguishable from tagged post-smolts using movement or depth data. Previous research has successfully determined ectothermic fish predation on smolts, largely due to the presence of reversals (Gibson et al. 2015), which would be uncharacteristic of an outmigrating salmonid. However, due to the complexity of the study site, ectothermic predation based on reversals is not likely useful, as post-smolts in both 2019 and 2021 were shown to temporarily reverse their direction multiple times (while still showing other typical post-smolt behaviours) as they migrated out of the study area. Alternatively, the depth sensor may allow for speculation on possible (albeit inconclusive) predation by ectothermic predators that typically reside in greater depths than salmonids, such as Atlantic cod (Thorstad et al. 2012a). In this study, the tag of eight post-smolts reported a depth greater than 5 m, which is below where Atlantic salmon post-smolts are typically observed (Renkawitz et al. 2012), without a corresponding change in temperature. However, these instances of abnormal depth readings without any temperature increase were not long-lasting, with most of these occurring during an ebb tide in highly turbid areas such as the Fundy Isles, Head Harbour Passage, and Western Passage (Figs. 1 and S7). Therefore, it can be assumed that these abnormally deep dives recorded are most likely a product of the migrating smolts being pulled deeper

by the tidal currents rather than evidence of ectothermic predation.

Salmon predation in estuarine and early marine environments has often focused on the impact of pinniped predation (Moore and Berejikian 2017, 2022), with some studies using techniques other than telemetry (Cronin et al. 2014; Gosch et al. 2014; Chasco et al. 2017b; Wargo Rub et al. 2019; Thomas et al. 2022). One method to estimate pinniped predation on salmon smolts is through the analysis of seal scat samples collected at haul-out sites or from digestive tracts from harvested animals. This method involves the recovery, identification, and measurement of hard parts (e.g., sagittal otoliths, cephalopod beaks, or invertebrate exoskeletons) to estimate prey weight and length and quantify diet composition. More recently, DNA-metabarcoding has also been used to identify diet composition (Thomas et al. 2017, 2022). Another common method in previous studies was the use of bioenergetic models. Bioenergetics models are mathematical models that estimate the energy requirements of an animal and the amount of food it needs to consume to meet those requirements. The combination of digestive tracts or scat analyses with bioenergetics models has been implemented on Pacific salmon species and can give rough estimations of the total number of outmigrating smolts that are consumed by pinnipeds (Lance et al. 2012; Howard et al. 2013; Chasco et al. 2017a). However, this requires a detectable level of salmon bones, otoliths, etc. within collected gut/scat samples, which may not be practical in areas such as the BoF, where salmon populations are so low. Additionally, in an area with significant aquaculture operations such as Passamaquoddy Bay, the differentiation between wild post-smolts and escaped farmed Atlantic salmon is difficult when analyzing DNA. Therefore, telemetry is likely the best option for detecting pinniped predation when salmon populations are low or migrating near salmon farms. However, the combination of a high number of receivers in a small, semi-enclosed environment such as Passamaquoddy Bay likely gives telemetry a greater advantage as a tool to assess marine mammal or bird predation on post-smolts than larger scale, more open areas such as the BoF or the Strait of Georgia, British Columbia.

The efficiency of the terminal arrays may have resulted in missed detections and a subsequent underestimation of the number of successful migrants. However, an underestimation of successful migrants would only decrease the percentage of overall marine mortality, resulting in similar conclusions that the endothermic predation in the early-marine environment does not contribute to significant mortality in this area. Missed detections at the terminal arrays would change the proportion of mortality explained by endothermic predators, but the overall endothermic predation percentages would remain the same. Additionally, the calculated array efficiency is based on the likelihood of a receiver missing a single transmitter ping. However, a post-smolt that is swimming past these terminal arrays would still be in the range of two receivers for a minimum of 330 m (based on a conservative 300 m detection range). Assuming a maximum swim speed of 1–2 ms^{-1} (to account for tidal currents) and a ping every 40 s, a tagged post-smolt would be expected to transmit at least four to five times within range of a receiver.

Due to the high ping rate of these tags, the 60% efficiency for detecting a single transmission becomes nearly 100% efficiency for detecting at least one of the pings during outmigration past this array. This likely covers possible missed detections of mammalian predators too, which typically cruise at slow enough speeds (i.e., <3 ms^{-1}; Hind and Gurney 1997) for multiple detections to be expected within receiver ranges. While it is difficult to combat long-lasting dips in receiver efficiency (i.e., tides), random leaks in the array are likely not a significant concern in this study.

The spacing between receivers limited our ability to pinpoint the precise locations of predation events. For example, one tagged post-smolt in 2021 (Tag ID: 1365883) had only 5 min between the last ambient temperature and its first 35 °C detections. Considering the tags used for this study transmitted every 20–40 s (40–80 s between two temperature transmissions), it would be expected that there would be more than two temperature detections, assuming the predation event occurred at that array and that transmissions were not missed due to environmental conditions or tag collisions. Therefore, predation may have occurred outside of receiver range, though likely not far for that fish. This is even more evident in other predation events, where the time between "last alive" and "first consumed" detections is over 1 h apart, meaning that several transmissions of temperature data occurred outside the range of receiver arrays. However, if we assume a swimming speed of one body length per second (BL s^{-1}) and use this in tandem with the time between "last alive" and "first consumed" detections, we can create a buffer around the "last alive" detection that represents the known area in which a predation event would have occurred. Layering these predation buffers allows for the depiction of predation hotspots (Fig. 4). This calculation highlights that Western Passage and Cobscook Bay are the most noticeable hotspots for marine mammal or bird predation during the smolt migration (Fig. 4). Using tighter arrays, increasing acoustic coverage near seal haul-outs, or higher frequency transmission could help mitigate uncertainties with species-specific dive patterns and predation locations. The array distribution for this study was more focused on exit passages—key points of interest (i.e., farms, seal haul-outs), and therefore areas of Passamaquoddy Bay (which could be very localized foraging areas for marine predators) could be lacking proper coverage to fully assess predation. A better understanding of tag retention and the timing of temperature increases upon consumption could also further improve predation estimates using telemetry.

Atlantic salmon populations have been in decline for decades, which is particularly apparent in their southern ranges, such as the BoF. The inner BoF Atlantic salmon populations are listed as endangered under the Species At Risk Act, with other populations, such as the outer BoF population examined in this study, considered threatened or facing historic recruitment lows throughout their range in Atlantic Canada (COSEWIC 2010). Consequently, research is ongoing to identify the factors most affecting migration and population dynamics to better understand their decline and develop successful recovery plans (Gibson et al. 2015). There is a need to more fully understand the drivers of Atlantic salmon mortal-

Fig. 4. Estimated endothermic predation hotspots for migrating post-smolts in Passamaquoddy Bay in 2019 and 2021. The location of predation events was determined by taking the maximum distance a smolt could have travelled in the time between the "last alive" and "first consumed" detections, using both (*a*) 0.5 BL s^{-1} and (*b*) 1.0 BL s^{-1}. All layers are projected in NAD83/UTM.
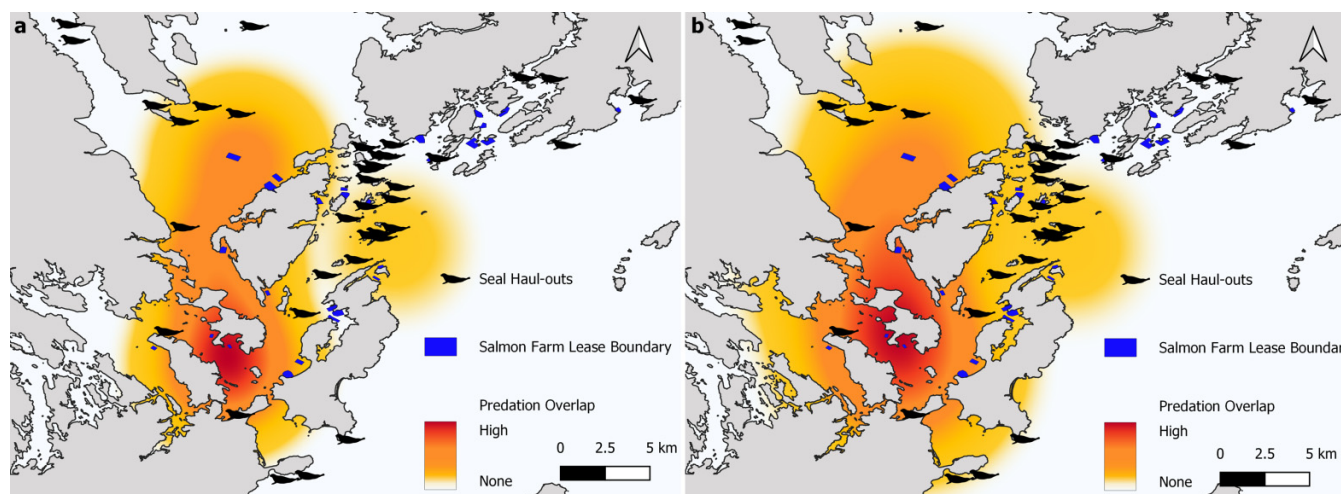
ity and pinpoint key phases where mortality is at its highest so that more meaningful recovery strategies can be designed and implemented. While current efforts such as river restoration are important, they are likely insufficient to recover Atlantic salmon populations from their current status if factors that affect their at-sea mortality rates are not addressed (ICES 2017; Lennox et al. 2021). Smolt-to-adult return rates for BoF vary between rivers but are generally estimated to be less than 1% (Lacroix 2008). It is thought that most of this is determined by mortality in the marine environment, with a 50% reduction in estuarine mortality only predicted to account for a 0.3% total increase in returning adults (Gibson et al. 2015). Our study helps highlight that outer BoF Atlantic salmon likely experience greater marine mortality during the longer at-sea phase than in the rapid early marine phase. More effort directed toward the offshore environment is needed to assess this at-sea mortality and determine potential factors, including predation (Cairns 2001; Seitz et al. 2019; Kennedy et al. 2023), low growth and poor prey quality (Mills et al. 2013; Renkawitz et al. 2015; Vollset et al. 2022), illegal, unreported, or unregulated fishing (Dadswell et al. 2022), or high prevalence of disease (Miller et al. 2014), among others. As acoustic telemetry equipment evolves, such as with increased transmitter power and frequency or the ability for transmitters to store data between receiver locations, the ability to characterize mortality events at the species level may improve. Only through a comprehensive understanding of the complex factors affecting Atlantic salmon populations can effective management strategies be implemented that ensure the survival of this species within the BoF and other regions experiencing similar declines.

Acknowledgements

Article information

History dates

Copyright

Data availability

Data generated or analyzed during this study are available from the Ocean Tracking Network (https://members.oceantrack.org/OTN/project?ccode=PBSM). Data are, however, available from the authors upon reasonable request.

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The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0206.

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