

1 Winter Ecology of Striped Bass (*Morone saxatilis*) Near its Northern  
2 Limit of Distribution in the Saint John River, New Brunswick

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4 Running head: **Striped Bass winter ecology**

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24 <A> **Abstract**

25 Winter habitat selection by Striped Bass (*Morone saxatilis*) has been described as  
26 opportunistic, but due to the length and severity of winter at its northern range, winter habitats in  
27 the north are predicted to be restricted in distribution and carefully selected. Here we describe the  
28 locations and environmental conditions supporting winter aggregations of adult Striped Bass  
29 including periods under ice cover in the Saint John River, New Brunswick using acoustic  
30 telemetry. Striped Bass of both Saint John River (72%) and other ancestry (28%) were observed  
31 to overwinter within the river's four mainstem lakes and embayments to which the individuals  
32 returned each fall. Most non-Saint John River ancestry Striped Bass were observed in habitats  
33 nearest the river mouth in winter. Striped Bass travelled to winter habitats from fall feeding  
34 locations from October to November, and only four tagged individuals departed the river at this  
35 time. Temperature, dissolved oxygen, and salinity conditions best described the winter habitats.  
36 By demonstrating the non-random distribution of Striped Bass during winter and identifying a  
37 gradient of habitat use by Saint John River ancestry Striped Bass in this northern river system, it  
38 is apparent that protection of these locations is critical for the long term conservation of Striped  
39 Bass populations in Canada.

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47 <A> **Introduction**

48           The native range of Striped Bass (*Morone saxatilis*) extends nearly 3000 km along the  
49 Atlantic Seaboard of North America from the St. John's River, Florida in the south to the St.  
50 Lawrence River, Québec in the North (Scott and Scott 1988). Populations occupying much of the  
51 species' principal range in central and northern regions must annually contend with winter  
52 periods lasting up to 7 months where temperatures are 0-4°C in fresh water to a depth averaged  
53 minimum of < -0.5°C reported for estuarine environments (Bradford et al. 1998, Andrews et al.  
54 2019a). Despite the long duration of the winter season, winter ecology remains a poorly  
55 described and infrequently studied aspect of Striped Bass habitats and life histories (Bednarski  
56 2007; Keyser et al. 2016; see review by Andrews et al. 2019a).

57           Striped Bass typically migrate to fixed wintering sites as water temperatures cool in late  
58 fall (reviewed by Andrews et al. 2019a). These winter locations can be sluggish river pools  
59 (Rulifson et al. 1987), sheltered inland harbours (Bednarski 2007), freshwater lakes (Bradford et  
60 al. 2012), and sometimes, coastal or offshore regions (Keyser et al. 2016). When water  
61 temperatures near winter minimums, Striped Bass are known to form dense aggregations  
62 (Bednarski 2007) and conduct minimal movements until water temperatures begin to warm in  
63 the spring at which time Striped Bass disperse. A reduction or complete cessation of feeding is  
64 suspected for Canadian populations (Dr. M. Dadswell, personal communication), though winter  
65 feeding may continue in more southern (Hudson River, Dunning et al. 1997; Chesapeake Bay,  
66 Hollis 1952) and/or coastal regions (Virginia and North Carolina Coast, Overton et al. 2008).  
67 Inland winter aggregations are suspected to occur primarily in sheltered habitats where the threat  
68 of displacement by tidal action, or runoff driven currents is minimal (Bradford et al. 2012), but  
69 how coastal winter habitats are selected and used remains poorly understood.

70 In this study, we use acoustic telemetry to monitor movements to and within Striped Bass  
71 winter habitats in the Saint John River (SJR), New Brunswick, from 2014-2018 (four  
72 consecutive winter periods). Monitored Striped Bass were determined to include both individuals  
73 of SJR ancestry and non-SJR ancestry that can co-occur in the river (Bentzen and Paterson 2008,  
74 Leblanc et al. 2018, Andrews et al. 2019a). It was predicted that environmental conditions at the  
75 onset and conclusion of winter dictated the migrations to and from repeated, *i.e.*, established  
76 overwintering sites. Within winter habitats, the under-ice conditions of temperature-, dissolved  
77 oxygen, and salinity regulated the Striped Bass aggregation and their patterns of movement. In  
78 Belleisle Bay where strong thermal stratification was observed, we hypothesize that stratification  
79 occurs in fall when large “spring tides” force still warm saline water from the lower estuary of  
80 the SJR over a shallow (1-3 m deep) delta at the mouth of Belleisle Bay after which it sinks into  
81 the bay’s deeper basin, a process known as ectogenic meromixis.

## 82 <A> Materials and Methods

### 83 <B> Study Area

84 The SJR is a 55,000 km<sup>2</sup> watershed that extends ~670 km from the Little Saint John Lake  
85 on the Maine-Québec border to the City of Saint John, New Brunswick, where it empties into the  
86 Bay of Fundy through a narrow opening (~100 m) known as Reversing Falls (Cunjak et al. 2011;  
87 Fig. 1). The head of tide extends to the city of Fredericton ~130 km upstream from the river  
88 mouth, and saltwater intrusion is measurable ~70 km upriver (to the village of Gagetown; Carter  
89 and Dadswell 1983; Fig. 1). Mactaquac Dam and Generating Station (MGS) is the most  
90 downstream located hydroelectric facility and presents a physical barrier to Striped Bass  
91 upstream migration and thus the upstream limit of our study area. In the downstream reach there  
92 are four large mainstem tributaries that join the SJR from the northeast (Fig. 1). Grand Lake and

93 Washademoak Lake provide freshwater lacustrine habitats (Carter and Dadswell 1983) while  
94 Belleisle Bay and Kennebecasis Bay are both closer to the river mouth and the Bay of Fundy and  
95 are characterised by greater tidal influence resulting in stratification from saltwater intrusions.  
96 During winter, much of the river becomes ice bound with small patches of open water in  
97 tributary mouths, lake thoroughfares, and at Reversing Falls due to extreme (8 m) tidal  
98 fluctuation.

99 The SJR is located near the northern extent of Striped Bass Atlantic distribution (Scott  
100 and Scott 1988) and hosts migrants from various population origins throughout the year, *i.e.*,  
101 SJR, Shubenacadie River, Nova Scotia, and the USA (Wirgin et al. 1995, Bentzen and Paterson  
102 2008, Leblanc et al., 2018, Leblanc et al. 2020). Winter habitats have been identified in all four  
103 major tributaries (Andrews et al. 2018a, 2018b, 2019a) and mixed ancestry winter aggregations  
104 in Belleisle Bay were previously reported by Bradford et al. (2001).

#### 105 <B> Tagging Methods

106 Adult Striped Bass (n=44, FL = 59 to 112 cm, weight = 3 to 20 kg) were captured at  
107 various locations within the SJR from 2013-2016 (Table I) using angling, commercial trap net,  
108 gill net, and the fish lift at the Mactaquac Dam. Individuals were anesthetized with clove oil  
109 (Eugenol) and surgically implanted with Vemco V13-4L (n=3; tag life=719 days), V16-4L  
110 (n=38; tag life=3650 days), and V16-6L (n=3; tag life =3650 days) acoustic tags. Tagging  
111 procedures followed those described in Wingate and Secor (2017) using a 40 mg/L solution of  
112 10-part ETOH:1-parts clove oil. Capture locations for this initial tagging group were chosen  
113 throughout the SJR to capture the broadest diversity of movements from Striped Bass varied  
114 ancestry and habitat origin. In 2017, an additional 19 Striped Bass (FL = 69 to 97 cm, weight = 5  
115 to 15 kg) were captured by angling directly downstream of the MGS in October and surgically

116 implanted with Vemco V16-4L (n=4; tag life = 3650 days) and V16-4H (n=15; tag life= 2305  
117 days) depth (0 to 34 m  $\pm$  1.7 m)/temperature (-5°C to 35°C  $\pm$  0.5°C) acoustic tags. Individuals  
118 fitted with depth/temperature tags were all captured and tagged at the MGS because Striped Bass  
119 occurring at this location were suspected (following observation of the initial tagging group) to  
120 disperse amongst overwintering locations in the fall.

121 During tagging scale samples were collected for ageing and a clip (1 cm<sup>2</sup>) of the caudal  
122 fin was collected for genetic analysis to determine ancestry (see Leblanc et al. 2018, Leblanc et  
123 al. 2020). Tag weight (range 9-16 g in water) was < 0.005% of fish weight in all cases and all  
124 tagging and sampling procedures were approved by the University of New Brunswick UNB  
125 Animal Care Committee (Animal Use Protocol Numbers 16026, 15024). Following tagging,  
126 Striped Bass with acoustic pinger tags (n= 37) and Pressure/temperature tags (n=16) were  
127 determined to have provided sufficient detections to resolve multi-year winter habitat occupancy  
128 (Table I).

### 129 <B> Tracking Methods

130 Tagged Striped Bass were tracked with a Vemco VR2W receiver array distributed along  
131 the SJR from the river mouth at Reversing Falls, upstream to the MGS (Fig. 2). The specific  
132 array included n=36 VR2W placements in 2014, 125 in 2015, 128 in 2016, 135 in 2017 and 58 in  
133 2018 (Fig. 2). Additional detection data were received from the Ocean Tracking Network (OTN  
134 - <http://oceantrackingnetwork.org/>). OTN receivers (n=19) detected tagged Striped Bass within  
135 the river in 2014, 17 in 2015, 48 in 2016, 9 in 2017, and 10 in 2018. OTN receivers (n=13) also  
136 detected Striped Bass outside of the SJR in 2014, 18 in 2015, 11 in 2016, 12 in 2017 and 22 in  
137 2018.

138 Manual winter tracking was also conducted from 2014-2017 using a Vemco VR100  
139 receiver from January-March when ice conditions were safe. The tracking procedure involved  
140 walking 50-300 m out from shore, drilling a hole through the ice with a hand or power auger and  
141 listening for tags using directional and omnidirectional hydrophones. This process was repeated  
142 every 1 km along the shore focusing on the river's main embayments. One-kilometer intervals  
143 were determined to be sufficient based on winter range testing with a tethered V16-4L acoustic  
144 range test tag tested at 8 depths (1.8-14.6 m) at ranges increasing at 100 m intervals from a  
145 VR100 receiver. The range test tag was clearly detected at distances > 1.5 km. In 2015, 92  
146 locations were manually surveyed with the VR100 receiver from Feb 2 – Mar 29 including in  
147 Grand lake (n=30), Washademoak Lake (n=10), Belleisle Bay (n=24), Kennebecasis Bay and  
148 Darling's Lake (n=17) and the main stem of the SJR (n=11). In 2016, 55 locations were surveyed  
149 from Jan 24 – Mar 30 including n=12, 12, 10, 15, 6, in Grand Lake, Washademoak Lake,  
150 Belleisle Bay, Kennebecasis River and the main SJR respectively. All tagged Striped Bass were  
151 located during each year either directly through manual tracking or were detected entering a river  
152 tributary or departing the SJR by a VR2W receiver. In some tributaries (*i.e.*, Grand Lake) the  
153 exact winter habitat of Striped Bass took multiple (2-3) winter seasons to locate.

154 Selected receivers occurring near Striped Bass winter aggregations in lakes were fitted  
155 with Onset HOBO® temperature pendants in 2014 (n=15), the majority of deployed receivers  
156 supported temperature loggers in subsequent years, (n=91) in 2015, (n=79) in 2016, and (n=93)  
157 in 2017 (receivers and associated temperature loggers deployed in 2017 remained in the water  
158 through spring 2018). Vertical temperature lines were deployed in areas of concentrated Striped  
159 Bass in winter in each lake/bay. Temperature lines were fitted with HOBO temperature pendants  
160 spaced at equal intervals of 2-5 m from the bottom to the surface and recorded temperatures

161 hourly. When winter habitats were safely accessible and after wintering Striped Bass had been  
162 located, water column profiles of conductivity ( $\mu\text{S}/\text{cm}$ ) and oxygen (%DO) were conducted  
163 using a YSI 6600 multimeric sonde,  $n=1-2$  per lake/season. These point measurements allowed  
164 for some observations to be made for winter habitats, but due to unstable ice conditions were  
165 conducted too infrequently to make regular comparisons with acoustic detections data.

#### 166 <B> Genetic Methods

167 All tagged Striped Bass ( $n= 63$ ) were genotyped. Sequencing methods are described in  
168 Leblanc et al. (2018), with the following exception: DNA isolation was performed using the  
169 E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Doraville, CA), ideal for processing small tissue  
170 amounts, or the high throughput NucleoMag® 96 Tissue kit (Machery-Nagel, Düren, Germany).  
171 Samples were prepared according to a modified double digest restriction-site associated DNA  
172 sequencing protocol originally developed by Poland et al. (2012), using restriction enzymes *PstI*  
173 and *MspI*. Sequencing protocol is detailed more fully in LeBlanc et al. (2018) and samples were  
174 analyzed using the same 1217 loci used in by LeBlanc et al. (2018). Individual samples were  
175 retained for genetic analysis if they had less than 30% missing data across all loci, to maximize  
176 number of individuals genotyped in each area.

177 Genetic structure of individuals was assessed using the R package LEA v. 2.0 (Frichot  
178 and François 2015), which performs least-squared estimates of the genetic ancestry of  
179 individuals without any *a priori* grouping. Simulations were run assuming 1 to 5 distinct  
180 ancestral populations, or genetic clusters, (K). The most likely K was chosen using a cross-  
181 entropy criterion, with the lowest minimal cross-entropy value considered the most probable  
182 (Frichot et al. 2014). The proportion of an individual's genome that resembles each genetic  
183 cluster is measured by the ancestry coefficient. Individuals with an ancestry coefficient greater

184 than 0.7 (70%) were said to belong to that genetic cluster, and those who were not assigned to  
185 any cluster were considered admixed, or hybrid fish. A threshold of 0.7 was chosen to  
186 complement the missing data threshold for individuals.

## 187 <A> Results

### 188 <B> Genetics:

189 A total of 42 Striped Bass from the SJR samples (67% of the 63 sampled) were  
190 successfully genotyped with <30% missing data across 1,217 loci and were compared to  
191 reference Striped Bass collected in Shubenacadie River, Miramichi River, Hudson River, and  
192 upper Chesapeake Bay stocks. The most likely number of genetic clusters (K) when including  
193 reference samples was found to be 4, which identified sampled fish as belonging to the SJR,  
194 Shubenacadie River, Miramichi River, SJR, and the United States samples.

195 Striped Bass sampled within the SJR originated from three different ancestries including  
196 the Shubenacadie River, Nova Scotia (n=9; 21%), USA stock (n=3; 7%) and a group of  
197 suspected SJR ancestry (n=26; 62%; See Leblanc et al. 2018, Andrews et al. 2019, Leblanc et al.  
198 2020). Striped Bass of Miramichi River origin as tested in the reference samples were not  
199 detected in the SJR. Additionally, n=3 individuals appeared to be admixed between individuals  
200 of USA and- SJR ancestry (7%), and one individual was admixed demonstrating SJR ancestry  
201 and both USA and Shubenacadie River ancestry.

202 In some cases, Striped Bass (n=7) that were not successfully genotyped or had > 30%  
203 missing data were provisionally assigned an origin based on migrations during the spawning  
204 period. Of these individuals of unconfirmed origin, (n=4) migrated to and were thus assumed to  
205 originate from the Shubenacadie River, and Striped Bass (n=3) were assumed to have SJR

206 ancestry as they were observed to migrate to a historic spawning location in the SJR near the  
207 City of Fredericton during each year of tracking (see also Andrews et al. 2019).

### 208 <B> Migration to Winter Habitats

209 In Oct-Nov tagged Striped Bass (n=49) were observed travelling to fixed locations we  
210 classified as overwintering sites within the SJR, additionally, four Striped Bass migrated to  
211 known overwintering sites in Nova Scotia/Minas Basin. Within the SJR, Striped Bass occupied  
212 Grand Lake (20%), Washademoak Lake (18%), Belleisle Bay (38%), and Kennebecasis River  
213 (18%) across all years. Furthermore, individuals were observed to return to the same winter  
214 location in each year of tracking regardless of genetic ancestry (exception, Tag ID: 24949,  
215 32652; see Table I)

216 In fall 26-38% of tagged Striped Bass congregated at the MGS to feed (see Andrews et  
217 al. 2018) prior to departing for winter habitat. Departure from the MGS occurred during a 16 –  
218 27-day period (mean = 21, SD  $\pm$  5) from Oct 15 - Nov 13, 2014-2017. The temperature at the  
219 time of departure ranged from 17.7 - 8.4°C (2015-2017), average = 13.6°C (SD  $\pm$ 2°C; F among years  
220 = 3.2, df = 1, p = 0.1).

221 Fall departure from the Kennebecasis River occurred from Oct 11 – Nov 24, 2015-2017,  
222 at a mean temperature of 8.5°C, SD  $\pm$  3.2°C. Departing Striped Bass (n=4 in 2015, 5 in 2016  
223 and 3 in 2017) all travelled to overwinter in Darling’s Lake (upstream end of Kennebecasis Bay;  
224 Fig. 1) except for one individual migrating to Belleisle Bay in 2015. Departure timing from other  
225 areas of the SJR, *i.e.*, Grand Lake and Oak Point (Fig. 1) ranged from Oct 31 – Nov 13, but there  
226 was insufficient data to describe the migrations and temperatures of departure for these Striped  
227 Bass.

### 228 <B> Winter Aggregations

229 From winter 2014/15-2017/18, 123 observations of winter habitat location were  
230 documented from the 53 tagged individuals for which movement data were available (Table I).  
231 Of these winter observations, 115 (93%) were documented within the SJR: n=23 in 2014, 25 in  
232 2015, 28 in 2016, and 39 in 2017 in four winter habitats: Belleisle Bay (n=47, 38%),  
233 Washademoak Lake (n=22, 18%), Grand Lake (n= 24, 20%), Darling's Lake (n=22, 18%; Fig.1).

234 Due to recurring multiyear residency in winter habitats by Striped Bass, proximal tagging  
235 to winter locations may bias assigned proportions. Thus, winter distribution based solely on  
236 individuals captured and tagged downstream of the MGS (Mactaquac or Mactaquac Hatchery;  
237 Table I) were also calculated to remove possible regional tagging bias. Using this method, 60%  
238 of Striped Bass occupied Belleisle Bay, 16% travelled to Washademoak Lake, 12% of Striped  
239 Bass spent the winter in Grand Lake, and 9% occurred in Darling's Lake (Fig. 1). Only 3% of  
240 tagged Striped Bass exited the SJR under this calculation method. In addition, considering only  
241 Striped Bass of SJR ancestry tagged at MGS, the proportions occupying each winter location  
242 was 68%, 24%, 8%, and 0% in Belleisle Bay, Washademoak Lake, Grand Lake, and Darling's  
243 Lake respectively.

#### 244 <C> Grand Lake

245 Striped Bass overwintering in Grand Lake (Table I) occupied a region of uniform depth  
246 ~8.5 m with 2 depressions of ~10 m depth near the northern end of the lake and upstream of the  
247 lake's single island (Goat Island). Striped Bass (n=3,1,4,3 tagged in 2014, 2015, 2016 and 2017,  
248 respectively) arrived in Grand Lake when temperature at the lake bottom (depth=8 m) was 7.0°C  
249 ± 3.3 (fall 2017). Striped Bass with depth/temperature sensing tags (n= 3 in 2017) were detected  
250 at a depth of 8.6 ± 1.37 m from January to May (Fig. 3) and tag temperatures were recorded as  
251 2.61 ± 0.98°C during this time. Water temperatures were approximately 0°C from the ice

252 surface to 7.5 m deep (n=3 readings), DO was >80% at the Lake bottom (~10m) (YSI sonde  
253 profile; February 28, 2017). Passive receiver arrays also suggest that Striped Bass may occupy  
254 habitat further towards the upstream end of Grand Lake periodically during winter. Striped Bass  
255 detected in Grand Lake over winter were of SJR ancestry (71%), admixed between SJR and USA  
256 stock (12%), or of unknown ancestry (17%; Fig. 1).

#### 257 <C> **Washademoak Lake**

258 Striped Bass overwintering in Washademoak Lake (Oct 14 – Nov 8 in fall to May 4-9 in spring;  
259 Fig. 4) were detected in the main lake basin from ~Oct 14 - Jan 2, 2016-2017 (mean=41 days)  
260 and more sporadically in 2017/2018 between Nov 4 – April 10 (mean =73 days). Tagged  
261 individuals then occupied an area (~4 m deep) in Washademoak Lake’s largest sheltered bay,  
262 Big Cove. This area was occupied from ~Dec 20 – May 3 in 2016/2017 (mean=126 days) and  
263 Dec 15 – May 9 in 2017/2018 (mean =95 days). In winter, water temperatures in Big Cove in  
264 Washademoak Lake dropped as low as 1°C (Dec -March) at which time Striped Bass appear to  
265 occupy depths 3.5-4 m. Striped Bass occupying Washademoak Lake are predominately of SJR  
266 river origin (82%, Fig. 1) and all individuals returned to Washademoak in each study year. Two  
267 individuals (Tag ID, 24949 and 32652) previously detected in Belleisle Bay during winter  
268 switched to the Washademoak Lake during one year of tracking (Table I). Detected Striped Bass  
269 of non-SJR ancestry were of Shubenacadie River origin (9%) or unknown origin (9%; Fig. 3,5)

#### 270 <C> **Belleisle Bay**

271 Belleisle Bay was the main wintering ground for Striped Bass throughout this study as  
272 the location sheltered 60% of tagged Striped Bass during winter (68% of SJR ancestry Striped  
273 Bass; Fig. 1). Striped Bass of non-SJR ancestry included 32% of Shubenacadie River origin, 2%  
274 of US ancestry and 2% of mixed ancestry. The origin of the remaining individuals could not be

Commented [SA1]: include percentages from other groups

275 determined. Striped Bass entered Belleisle Bay in late fall (Oct 16 – Nov 5; 2016-2018) after  
276 which they aggregated near the geographic centre of the bay. Some movement along the bay  
277 during winter was also observed.

278 Striped Bass in Belleisle Bay occupied warm waters resulting from tidally driven  
279 ectogenic meromixis (occurring when salt water from outside origin enters a lake or embayment,  
280 settles to the bottom and maintains a stable thermocline between deep saline waters and surface  
281 fresh waters, Hakala 2004; Fig. 6) in 2 out of 3 study years for which temperature profiles were  
282 available (2016-17 and 2017-18). In those years winter temperatures were as warm as 14.1°C on  
283 Dec 1 and 11.8°C on May 1, in 2016, and 14.2°C on Dec 1 and 10.3°C on May 1 in 2017, as  
284 recorded at depths >15 m and salinities of 2.5-4.6 ppt. Due to the warm water or perhaps  
285 reduced circulation, oxygen was < 60% saturation at depths >18 m, and as a result, Striped Bass  
286 were possibly subject to an inverse temperature oxygen squeeze (see Countant 1985). Striped  
287 Bass thus occupied a median depth of 15 m from Dec to March where a median temperature of  
288 8.8°C was record from December through February cooling to 7.8°C in March; DO% saturation  
289 was >80% at 15 m depth in the same time period (Fig. 6).

290 Striped Bass that occupied Belleisle Bay over winter returned to this location in each year  
291 of the study. One individual; however, (32652; Table I) was documented switching to overwinter  
292 in Washademoak Lake where it may have been captured or died in early spring. Striped Bass  
293 remain in Belleisle Bay until (May 15; 2016-2018; Fig. 5) when they departed to spawning  
294 habitats. Departure from Belleisle Bay appears to coincide with a rapid increase in water level  
295 and surface water temperature during spring freshets in the SJR when surface waters of Belleisle  
296 Bay warm rapidly and ice cover melts.

297

298 **<C> Darling’s Lake**

299 No Striped Bass that occupied Darling’s Lake from 2014-2018 were of confirmed SJR  
300 ancestry, however, one SJR/USA admixed individual observed in three years (2015-2017) and  
301 accounting for 14% of winter observations was confirmed. Most Striped Bass occupying this  
302 habitat throughout the study were from the USA (19%) or Shubenacadie River (24%; Fig. 1)  
303 while the remainder (43%) were of unknown origin and made no clear spawning migration in  
304 spring.

305 Striped Bass occupying Darling’s Lake are the only group to which two entry points were  
306 available for access to winter habitat and the use of these entries in both fall and spring was  
307 predictable. Upon entering the overwintering location in the fall (Nov 5 – Nov 28), Striped Bass  
308 (100% in 2015, 83% in 2016 and 83% in 2017) were tracked first arriving via the downstream  
309 entrance of the lake where it meets the Hammond River. When departing in the spring (April 11  
310 – May 3) across all years, Striped Bass (75% in 2016, 67% in 2017 and 67% in 2018) were  
311 recorded exiting through the northern (upstream) entrance to the lake (Fig. 7). Furthermore, each  
312 tracked individual entered and exited the lake in same pattern each year (differences in  
313 percentages are due to newly tagged fish and winter mortalities).

314 Darling’s Lake provided the smallest area of Striped Bass winter refuge on the SJR (0.6  
315 km<sup>2</sup> >3.5 m deep). Water temperatures from 0-2 m depth were 0.08 - 0.43°C in 2015 but  
316 increased to 2.34 – 2.86°C from 3 – 4.76 m in depth. Temperatures as low as 0.1°C were  
317 recorded throughout the water column on Dec 14, 2017. Oxygen saturation was 69 - 45%  
318 measured from 3 – 4.76 m depth, though remained between 86 - 77% at depths <3 m.

319

320 **<B> Overwintering outside of the Saint John River**

321           Only four Striped Bass (8% of the total detected) departed from the SJR in the fall and all  
322 were determined to be of Shubenacadie River ancestry (Fig. 1). Three of these individuals  
323 travelled to and resided in Minas passage in winter of 2017 (Nov 20 – Mar 31; see Keyser et al.  
324 2016). Two carried pressure temperature tags which showed they occupied depths from 3.94 m  
325 to >34 m (tags could only read a depth range of 0-34 m and Striped Bass may have occupied  
326 deeper sections of the water column) and temperatures ranging from 11.16°C in November to  
327 1.58°C in late March. Two tagged fish (Tag ID 32652, and 24960 in 2014-2016) were detected  
328 passing through the Minas Passage in late fall (2014-2016); their true wintering location (likely  
329 somewhere in Minas Basin/Nova Scotia) could not be determined. Those same individuals  
330 arrived back in the SJR in early summer (July 4 – August 11; 2015-2018) after the typical  
331 Striped Bass spawning period in the Shubenacadie River (May 16- June 9, Rulifson and  
332 Dadswell 1995; Paramore and Rulifson 2001, Duston et al 2018).

333 **<B> Departure from Winter habitat in the spring**

334           Striped Bass appear to depart winter habitats within the SJR when waters begin to warm  
335 in the spring and turnover events occur. In Grand Lake departure times varied from April 3 –  
336 May 28 (water temperature 3.5 – 13.5°C measured at ~6 m depth measured in 2018) with a mean  
337 departure date of May 5 (6.2°C). In Washademoak Lake, Striped Bass departed from April 8 –  
338 May 9 (2016-2018) with a mean departure date of April 21. Water temperature at these times  
339 ranged 4.5 - 9.2°C from the surface to waters 9 m deep. In Belleisle Bay all Striped Bass  
340 departed by May 15<sup>th</sup> in each year of tracking when water temperatures were recorded as 8.0-  
341 9.7°C throughout the water column. Belleisle Bay was the most upstream location with a  
342 moderate proportion of Shubenacadie River origin Striped Bass and those individuals were  
343 observed to depart prior to May 1 (*i.e.*, ahead Striped Bass of SJR ancestry) in 2016 (mean =6°C)

344 and 2017 (mean=4.3°C). Striped Bass of Shubenacadie ancestry had all departed by May 7 in  
345 2018 at an average temperature of 7.0°C. Darling's Lake was predominately occupied by  
346 Striped Bass of non-SJR ancestry (*i.e.*, Shubenacadie and US) and those individuals were  
347 observed to depart from the lake April 11 -May 3 when water column temperatures exceeded  
348 5°C, though few (n=2) were subsequently observed to depart from the river.

349

#### 350 <A> Discussion

351 During winter in the SJR, Striped Bass occupied warmer (2-7°C), oxygenated (> 60%  
352 DO), low salinity (< 4.6 ppt) and sheltered (either within coves, or below stratified water layers)  
353 habitats to which individuals returned throughout the four winters of the study. Most Striped  
354 Bass, 60%, returned each year to winter in Belleisle. These adults were a mix of SJR,  
355 Shubenacadie, and USA ancestry. Interestingly, most SJR ancestry Striped Bass wintered  
356 farthest upriver (Grand Lake and Washademoak lakes), with greater proportions of mixed  
357 ancestry aggregations occurring closer to the river mouth. An additional finding was the fidelity  
358 to the SJR and its wintering habitats by non-SJR ancestry Striped Bass which suggests individual  
359 stocks may be more dependant on stable long-term habitats in non-natal rivers than previously  
360 suspected.

361 Adult Shubenacadie origin Striped Bass have been detected in SJR winter habitats  
362 (Bradford et al. 2001), but their fidelity to those winter habitats was neither documented nor  
363 suspected. Striped Bass <age-3 do not commonly depart home rivers (Greene et al. 2009);  
364 therefore, they are predicted to become accustomed to overwintering near, or within their natal  
365 rivers. Young-of-the-year Striped Bass of Shubenacadie River ancestry; however, have been  
366 documented in the Petitcodiac River (>200 km from the Shubenacadie River; Dustin et al. 2018)

367 and could find their way to the SJR at an early age. Alternatively, the increasing size of the  
368 Shubenacadie River population (COSEWIC 2012), and evidence of changing winter habitat  
369 selection in individuals from that population (Gemperline et al. 2002) suggests that adults  
370 occasionally emigrate from the Shubenacadie River to seek new winter habitats, e.g., the SJR or  
371 Minas Passage (see Keyser et al. 2018). Dispersal mechanisms do exist *i.e.*, migratory groups,  
372 increasing population, and individual size (Waldman et al. 1990) and could possibly explain the  
373 occurrence of Shubenacadie Striped Bass in the SJR overwinter, but this does not explain the  
374 reoccurring wintering of these individuals in the SJR now observed. Similarly, Striped Bass with  
375 USA ancestry were documented re-occupying winter habitats within the SJR through the study  
376 and furthermore remained in the river in spring during the spawning period.

377         Of the winter habitats occupied in the SJR, Belleisle Bay was by far the most frequently  
378 utilized location, sheltering ~60% of all Striped Bass amongst study years (Fig. 1). This high  
379 rate of occupancy of Belleisle Bay occurred despite no Striped Bass being tagged in this location.  
380 Belleisle Bay is also the farthest winter habitat from all possible spawning locations (see  
381 Andrews et al. 2020) which would be the source of juveniles with SJR Ancestry and thus they  
382 appear to bypass closer winter habitats in favour of this location. The high rate of occupancy in  
383 Belleisle Bay is likely due to the strong thermal stratification and the related DO and salinity  
384 stratification observed in most years attracting Striped Bass of SJR and non-SJR ancestry. The  
385 winter conditions selected by Striped Bass throughout the SJR were well defined which also  
386 suggests a limited availability of necessary winter habitats but strong stratification within  
387 Belleisle may offer large expanses of “sheltered” habitat occurring below the halocline that could  
388 be attractive to Striped Bass regardless of temperature.

389 Striped Bass appear to select sheltered locations which either occurred below the  
390 thermo/halocline or within coves in order to avoid tidal movement and secondarily select the  
391 warmest available water providing sufficient oxygen is available *i.e.*, >80%. Striped Bass may  
392 also be affected by rain events during winter that alter their exiting winter conditions, *i.e.*, runoff  
393 of freshwater (Chaisson et al. 2002). Striped Bass in this study appeared to move downstream  
394 following large rainfall events and the subsequent increase in river discharge. The downstream  
395 movement may have been the result of physical displacement following increased river  
396 discharges or the added freshwater may have altered river salinities or temperature causing  
397 Striped Bass to move in response. Further evidence of the environmental control of habitat was  
398 observed in spring when departure from the winter habitat coincided with the dissipation of the  
399 cold surface waters and loss of thermal stratification. Overall, the evidence suggests that winter  
400 habitats in northern waters are very well defined and limited and in the case of the SJR are not  
401 occupied opportunistically.

402

#### 403 <A> Conclusion

404 The SJR offers a rare opportunity for comparison of multiple, distinct Striped Bass stocks  
405 and their winter habitats. We demonstrated that Striped Bass of SJR ancestry seek out the same  
406 overwintering locations annually in the SJR beginning as early as age-2 (Andrews et al. 2020b).  
407 Interestingly, this behaviour also holds true for Striped Bass of non-SJR ancestry with all bass of  
408 various ancestries (*i.e.*, Shubenacadie, USA) returning to specific river habitats across all years  
409 of monitoring. This observation suggests winter habitat fidelity driven by persistent  
410 environmental conditions is another component of the known fidelity to natal rivers. Belleisle  
411 Bay was favoured as winter habitat most probably because of its stratified

412 warm/saline/oxygenated water, and this bay has a well established and long-documented winter  
413 presence of Striped Bass (Reviewed in Andrews et al., 2017).

414         Given the high use and fidelity to the winter habitats we observed, the heavy commercial  
415 fishing on overwintering habitats, particularly Belleisle Bay occurring until 1978 (Andrews et al.  
416 2017) may have historically resulted in near extirpation of the 68% of SJR ancestry Striped Bass  
417 observed to occupy that location. Winter habitat fidelity to other regions of the SJR, namely  
418 Grand Lake; however, may have spared the entire SJR stock from collapse notwithstanding  
419 subsequent impacts imposed by the Mactaquac Dam (see Andrews et al. 2020).

420         The results of this study should prompt managers to examine the sustainability of current  
421 and future Striped Bass commercial and recreational fisheries throughout the species range  
422 which may inadvertently target distinct winter contingents instead of the overall Striped Bass  
423 stocks. Depending on location and stock origin fixed gear fisheries occurring near known winter  
424 habitats may impart significant localised effects on multi ancestry stocks with unknown effects.

425

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427

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431 the Hampton Marsh and Kennebecasis River. Finally, we would like to thank NSERC CRDPJ  
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564 Table I: Biometric table for acoustically tagged Striped Bass including their annual winter  
565 location within and exterior to the Saint John River over four years of tracking (2014-2018).  
566 Genetic origin is also displayed as SJR (Saint John River ancestry), SHUB (Shubenacadie River,  
567 Nova Scotia), USA (United States origin) or admixed (SJR/US). Genetic Origins followed by  
568 “?” had too much missing data to assign true population of origin but the origin was inferred  
569 based on chosen spring spawning locations (i.e., SHUB? Individuals travelled to the

570 Shubenacadie river NS during each spawning period, SJR? Individuals travelled to Fredericton,  
 571 NB). Striped Bass that died or were undetected following tagging (n=10) were omitted from the  
 572 table. Striped Bass are sorted by tagging date and overwintering location. Note: two individuals  
 573 switched from Belleisle Bay to Washademoak Lake each in one year of tracking, they are  
 574 marked in dark grey.  
 575

	Tag ID	Tagging date	Tagging location	FL (cm)	Weight (kg)	Genetic Origin	2014/2015 Winter location	2015/2016 Winter location	2016/2017 Winter location	2017/2018 Winter location
Grand Lake	32646	2014-05-23	Grand Lake	72.5	5.35	SJR	Grand Lake	Died in Grand Lake in winter 2015/16		
	24952	2014-06-11	Grand Lake	67.4	3.95	SJR	Grand Lake	Grand Lake	Grand Lake	Grand Lake
	24942	2014-07-16	Mactaquac Hatchery	73	5.62		Grand Lake	Grand Lake	Grand Lake	Grand Lake
	22139	2015-06-15	Grand Lake	61	3.36	SJR?		Grand Lake	Grand Lake	Grand Lake
	22138	2016-05-11	Flowers Cove	73	5.20	SJR			Grand Lake	Grand Lake
	21323	2016-05-11	Flowers Cove	68	4.13	SJR			Grand Lake	Grand Lake
	21324	2016-05-11	Flowers Cove	71	4.59	SJR			Grand Lake	Grand Lake
	21328	2016-05-20	Grand Lake	66	3.00	SJR/US			Grand Lake	Grand Lake
	11242	2017-10-14	Mactaquac	97	8.02	SJR/US				Grand Lake
	11232	2017-10-25	Mactaquac	90	10.64	SJR				Grand Lake
11430	2017-10-26	Mactaquac	97	15.04	SJR				Grand Lake	
Washademoak	24951	2014-06-11	Grand Lake	78.4	7.08	SJR	Washademoak	Washademoak	Washademoak	Captured at Mactaquac
	24946	2014-08-21	Mactaquac hatchery	76	6.53	SJR?	Washademoak	Washademoak	Washademoak	Washademoak
	24944	2014-08-22	Mactaquac hatchery	76	4.94	SJR	Washademoak	Washademoak	Washademoak	Washademoak
	21326	2015-10-24	Washademoak	79	6.40	SJR		Washademoak	Washademoak	Washademoak
	22132	2015-10-24	Washademoak	79	7.03	SJR		Washademoak	Washademoak	Washademoak
	22135	2016-05-27	Grand Lake	94	12.35				Washademoak	Washademoak
	11250	2017-10-23	Mactaquac	79	6.27	SJR				Washademoak
	32645	2013-10-04	Mactaquac hatchery	83.6	9.30		Belleisle Bay	Died in Belleisle Bay in winter 2015/16		
32647	2013-10-04	Mactaquac hatchery	76.5	6.52	SHUB?	Belleisle Bay	Belleisle Bay	Belleisle Bay	Belleisle Bay	
32648	2013-10-04	Mactaquac hatchery	90.9	9.66	US	Belleisle Bay	Captured in Bay of Fundy?			
24949	2014-06-11	Grand Lake	76.6	6.58	SHUB?	Belleisle Bay	Washademoak	Belleisle Bay	Belleisle Bay	
22136	2015-06-20	Hampton Marsh	94	9.34	SJR		Died in Belleisle Bay in winter 2014/15			
24948	2014-08-22	Mactaquac hatchery	67.6	4.54	SJR	Belleisle Bay	Belleisle Bay	Belleisle Bay	Belleisle Bay	
24950	2014-08-22	Mactaquac hatchery	69.3	4.49	SJR?	Belleisle Bay	Belleisle Bay	Belleisle Bay	Belleisle Bay	
24953	2014-08-22	Mactaquac hatchery	85	9.25	SJR	Belleisle Bay	Died in Belleisle Bay in winter 2015/16			
24954	2014-09-12	Mactaquac hatchery	80	7.35	SJR	Belleisle Bay	Belleisle Bay	Belleisle Bay	Belleisle Bay	
24956	2014-09-12	Mactaquac hatchery	77.5	6.40	SJR	Belleisle Bay	Belleisle Bay	Belleisle Bay	Belleisle Bay	
24958	2014-09-13	Reversing Falls	81.5	7.48	SHUB	Belleisle Bay	Belleisle Bay	Belleisle Bay	Captured in Bay of Fundy	
32652	2014-09-13	Reversing falls	75.8	4.94	SHUB?	Belleisle Bay	Belleisle Bay	Died in Washademoak in winter 2016		
22141	2015-06-10	Grand Lake	68	5.76	SJR		Belleisle Bay	Belleisle Bay	Belleisle Bay	
11254	2017-10-14	Mactaquac	76	5.46	SJR/US				Belleisle Bay	
11258	2017-10-15	Mactaquac	95	11.97	SJR				Died in Belleisle in winter 2017/18	
11256	2017-10-15	Mactaquac	89.5	9.47	SHUB				Belleisle Bay	
11252	2017-10-23	Mactaquac	83	7.3	SJR				Belleisle Bay	

	11240	2017-10-25	Mactaquac	77	7.18	SJR				Died in Belleisle in winter 2017/18
	11238	2017-10-25	Mactaquac	76	7.28	SJR?				Belleisle Bay
	11246	2017-10-25	Mactaquac	83	8.89	SHUB				Belleisle Bay
	11230	2017-10-25	Mactaquac	77	6.35	SJR				Belleisle Bay
	11234	2017-10-25	Mactaquac	82	10.27	SJR				Belleisle Bay
	11426	2017-10-25	Mactaquac	88	10.11	SHUB				Belleisle Bay
Darling's lake	24941	2014-07-25	Hampton Marsh	95.2	10.52		Darling's Lake	Darling's Lake	Darling's Lake	Darling's Lake
	24943	2014-07-25	Hampton Marsh	100	13.79		Darling's Lake	Darling's Lake	Darling's Lake	Darling's Lake
	24945	2014-07-25	Hampton Marsh	112	19.60		Darling's Lake	Died in Darling's Lake in winter 2015/16		
	24959	2014-09-12	Mactaquac hatchery	77.5	6.03	SHUB?	Darling's Lake	Died at reversing falls, catch and release?		
	24957	2014-09-12	Mactaquac hatchery	80.8	7.67	SHUB?	Darling's Lake	Darling's Lake	Darling's Lake	Darling's Lake
	22137	2015-06-15	Grand Lake	74	5.03	SJR/US		Darling's Lake	Darling's Lake	Darling's Lake
	22133	2016-06-09	Hampton Marsh	79	7.06	US			Darling's Lake	Darling's Lake
	24945*	2016-06-17	Hampton Marsh	112	19.83	US			Darling's Lake	Darling's Lake
Outside SJR	32650	2014-06-09	Hampton Marsh	58.7	2.95	SHUB?	Outside SJR	Outside SJR	Captured or did not return to SJR	
	24960	2014-09-13	Reversing Falls	83.7	7.71	SHUB?	Outside SJR	Outside SJR	Outside SJR	Minas Passage
	11428	2017-10-15	Mactaquac	93	11.33	SHUB				Minas Passage
	11244	2017-10-25	Mactaquac	80	7.33	SHUB				Minas Passage

576  
577 \*Striped Bass 24945 tagged in 2014-07-25 died overwinter in Darling's lake in 2016, this same

578 tag (denoted as 24945a) was re-implanted into a Striped Bass on 2016-06-17

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580

581 Figure 1: The lower Saint John River, New Brunswick including the four major tributaries with  
582 Striped Bass winter aggregations in 2014-2017 including overall percentages of all tracked  
583 Striped Bass at each location calculated from individuals tagged at Mactaquac Dam. Proportions  
584 of Striped Bass of each identified stock ancestry occupying each winter habitat are graphically  
585 denoted. Saint John River ancestry (blue), suspected Saint John River ancestry (blue stipple),  
586 Shubenacadie River ancestry (green), suspected Shubenacadie River ancestry (green stipple),  
587 United States ancestry (yellow), USA/SJR admixed (yellow/blue stripe) and unknown (grey). All  
588 Striped Bass departing from the Saint John River prior to winter were of known (n=2) or  
589 suspected (n=2) Shubenacadie River origin.

590

591 Figure 2: Locations of Striped Bass tagging (fish symbols), project specific VR2W receiver  
592 placements (black points), and OTN receivers (black open circles) which detected tagged Striped  
593 Bass along the Saint John River, New Brunswick from 2014-2018.

594

595 Figure 3: Striped Bass winter activity in Grand Lake, Saint John River, New Brunswick: Panels  
596 (A) 2015-16; (B) 2016-17; and (C) 2017-18. Panels 1(A-C) show the receiver locations at points  
597 with a line to match panels 2 (A-C) and river kilometers. Panels 2 (A-C) are density isopleths of  
598 mean hourly upstream location (n=6332 (A), 16816 (B), and 14044 (C) points) for detected  
599 individuals, the outermost contour is the 90% isopleth. Horizontal lines correspond to receivers  
600 in panels 1 (A-C). Panels 3 (A-C) are the winter residency times for individual detected Striped  
601 Bass including date and water temperature of first and last detection, blue lines indicate Striped  
602 Bass of Saint John River ancestry or SJR/USA admixed individuals, grey line indicates Striped  
603 Bass of unknown ancestry. Panel 4 (C) is water temperature of Grand Lake over winter recorded  
604 continuously at a receiver in the wintering ground at 7 m depth. Note: This figure contains data  
605 from Striped Bass tagged from 2013-2016 (*i.e.*, non-sensor acoustic tags) only.

606

607 Figure 4: Striped Bass winter activity in Washademoak Lake, Saint John River, New Brunswick:  
608 Panels (A) 2015-16; (B) 2016-17; and (C) 2017-18. Panels 1(A-C) show the receiver locations at  
609 points with a line to match panels 2 (A-C) and river kilometers. Panels 2 (A-C) are density  
610 isopleths of mean hourly upstream location (n=7403 (A), 22537 (B), and 16907 (C) points) for  
611 detected individuals, the outermost contour is the 90% isopleth. Horizontal lines correspond to  
612 receivers in panels 1 (A-C). Panels 3 (A-C) are the winter residency times of detected Striped  
613 Bass including date and water temperature of first and last detection, blue lines indicate Striped

614 Bass of Saint John River ancestry, green are Shubenacadie River ancestry and the greys lines  
615 represents Striped Bass of unknown ancestry. Panel 4 (C) is water temperature of Washademoak  
616 Lake over winter recorded continuously on a temperature line (star point, panel 1A, 1B) and  
617 receiver stationed at 5 m depth at river km 76 (C). Note: This figure contains data from Striped  
618 Bass tagged from 2013-2016 (*i.e.*, non-sensor acoustic tags) only.

619  
620 Figure 5: Striped Bass winter activity in Belleisle Bay, Saint John River, New Brunswick: Panels  
621 (A) 2015-16; (B) 2016-17; and (C) 2017-18. Panels 1(A-C) show the receiver locations at points  
622 with a line to match panels 2 (A-C) and river kilometers. Panels 2 (A-C) are density isopleths of  
623 mean hourly river kms (n=27480 (A), 18561 (B), and 19891(C) points) for detected individuals,  
624 the outermost contour is the 90% isopleth. Horizontal lines correspond to receivers in panels 1  
625 (A-C). Panels 3 (A-C) are the winter residency times of detected Striped Bass including date and  
626 water temperature of first and last detection, blue lines indicate Striped Bass of Saint John River  
627 ancestry and green lines are Shubenacadie River ancestry individuals. Panel 4 (C) is water  
628 temperature of Belleisle Bay over winter recorded continuously on a temperature line at star  
629 points on panels 1(A-C). Winter 2016/2017 and 2017/2018 exhibit ectogenic meromixis with  
630 saline bottom layers remaining near 13°C despite surface ice cover. Note: This figure contains  
631 data from Striped Bass tagged from 2013-2016 (*i.e.*, non-sensor acoustic tags) only.

632  
633 Figure 6: Vertical movement of a single Striped Bass tagged with a pressure and temperature  
634 sensing tag (black dotted line; Tag ID: 22138) occupying Belleisle Bay Oct 28-May 3, 2017-18.  
635 Black and grey lines represent the average daily minimum, maximum and median depth of all  
636 pressure/temperature tagged Striped Bass detected in Belleisle Bay over winter (n=8, 2017-

637 2018). Temperature (°C, indicated by colour scale) was measured continuously at 1-hour  
638 intervals across the winter season using a temperature logger string (loggers positioned at  
639 6,9,12,15,18,21,24,27,30.5 m depth; Latitude 45.59076, Longitude -65.93513). The white band  
640 at the top of the chart (surface) indicates missing temperature data from 0-6m near surface ice  
641 cover.

642

643 Figure 7: Striped Bass winter activity in Darling's Lake, Saint John River, New Brunswick:  
644 Panels (A) 2015-16; (B) 2016-17; and (C) 2017-18. Panels 1(A-C) show the receiver locations at  
645 points with a line to match panels 2 (A-C) and river kilometers. Panels 2 (A-C) are density  
646 isopleths of mean hourly river kms (n=12557 (A), 19820 (B), and 18272 (C) points) for detected  
647 individuals, the outermost contour is the 90% isopleth. Horizontal lines correspond to receivers  
648 in panels 1 (A-C). Panels 3 (A-C) are the winter residency times of detected Striped Bass  
649 including date and water temperature of first and last detection, blue lines indicate SJR/USA  
650 admixed Striped Bass, green lines indicate Striped Bass of Shubenacadie River ancestry, yellow  
651 are USA ancestry and grey lines are Striped Bass of unknown ancestry. Circle and Triangle  
652 points on panel 3 (A-C) indicate entry and exit route to and from Darling's Lake. Panel 4 (C) is  
653 water temperature of Darling's Lake over winter recorded continuously on a temperature line  
654 (temperature line located at Star point on panel 1 A-C). Note: This figure contains data from  
655 Striped Bass tagged from 2013-2016 (*i.e.*, non-sensor acoustic tags) only. Striped Bass tag ID  
656 24945 in panel A3 died in winter (black point), this same tag was re-implanted in Striped Bass  
657 24945\* that was detected in 2016-17, 2017-18.



**DSPACE**

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**Winter ecology of striped bass (*Morone saxatilis*) near its northern limit of distribution in the Saint John River, New Brunswick**

**Andrews, S. N.; Linnansaari, T.; Curry, R. A.; Leblanc, N. M.; Pavey, S. A.**

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