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Title: Informing conservation strategies for the endangered Atlantic sturgeon using acoustic telemetry and multi-state mark-recapture models

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27 **Summary**

- 28 1. Causes of non-intentional mortality may pose conservation challenges for long-lived,
29 migratory species. Recovery attempts for Atlantic sturgeon *Acipenser oxyrinchus*
30 *oxyrinchus* populations in the USA have mainly involved closures of targeted fishing, but
31 bycatch mortality from fisheries targeting other species remains a significant obstacle.
32 Natural and fishing mortality levels are highly uncertain and difficult to separate, but
33 quantifying spatial and temporal patterns of movements and total mortality can directly
34 inform management policies regarding fishing activity that affects sturgeon.
- 35 2. Sub-adult sturgeon were tagged with acoustic transmitters to track their movements with
36 receivers deployed in active fishing areas within the New York Bight. Multi-state mark-
37 recapture models were used to quantify seasonal patterns in survival and migration while
38 accounting for detection probabilities of tagged fish.
- 39 3. Movement patterns of sturgeon were highly variable among seasons along the Long
40 Island Coast, with frequent south-westward movements during the increase in sea surface
41 temperature in spring. North-eastward movements were most pronounced during winter,
42 when temperatures were lowest. Sturgeon were less common along coastal Long Island
43 during summer.
- 44 4. Larger fish transitioned among strata more frequently, but also had slightly lower
45 survival than smaller fish which may result from selectivity for larger individuals caught
46 incidentally in bottom trawl or gillnet fisheries. Weekly total mortality rates, including
47 both natural and fishing mortality, averaged 0.24%. Highest weekly survival rates were
48 observed during periods of decreasing sea surface temperature in autumn and winter,
49 while lowest survival was observed during periods of increasing temperature in spring
50 and summer while sturgeon migrated through areas of known bycatch.
- 51 5. *Policy implications.* Movement and survival patterns of Atlantic sturgeon suggest that
52 late spring, coinciding with periods of high ocean bycatch in fisheries along the coast of
53 Long Island, is a particularly sensitive period for Atlantic sturgeon. Conservation efforts
54 could target these few weeks using real-time observations from acoustic telemetry and

55 remote sensing technologies to implement in-season fishery closures, thereby reducing
56 incidental mortality of Atlantic sturgeon. Such bycatch management measures would aid
57 in recovery attempts of a long-lived, migratory population with endangered status.

58 **Key-words**

59 *Acipenser*; animal movement; biotelemetry; bycatch mortality; capture-recapture; fishery
60 closure; migration; model selection; population recovery; survival rate

61 **Introduction**

62 Management of living resources generally seeks to balance the abundance and mortality of
63 populations to achieve sustainable exploitation. If populations are driven to low abundance,
64 mortality rates must usually be reduced to allow recovery. This is particularly challenging with
65 long-lived species (Heppell *et al.* 2005; Jarić, Gessner & Lenhardt 2015) because mortality from
66 anthropogenic factors accumulates during pre-adult life stages. Migrations pose further
67 conservation challenges for some species as individuals are exposed to various stressors along
68 habitats encountered. If critical mortality periods can be identified for populations in need of
69 rebuilding, then spatio-temporal management approaches implemented at appropriate ecological
70 scales (Dunn *et al.* 2016) may reduce mortality, even for long-lived and migrating species.

71 Conservation concerns have developed for Atlantic sturgeon *Acipenser oxyrinchus*
72 *oxyrinchus* (Mitchill, 1815) populations along the east coast of North America that led to
73 threatened or endangered listings in U.S. waters (USOFR 2012). Depressed population
74 abundances resulting from two pulses of directed fishing in the late 1800s and late 1900s,
75 combined with other factors including habitat loss (Smith 1985) and pollution (Chambers *et al.*
76 2012), led to a 1998 moratorium on targeted fishing. Despite the moratorium, populations
77 continued to decline. One possible explanation for the lack of rebuilding is that sturgeon are still
78 taken as bycatch (i.e. incidental catch in non-target fisheries) in marine fisheries operating along
79 the U.S. Atlantic Coast (Stein, Friedland & Sutherland 2004; ASMFC 2007; Neat *et al.* 2014;
80 Dunton *et al.* 2015). The timing of coastal migration periods strongly influences fishing
81 mortality because of the spatio-temporal overlap with fishing activity (Dunton *et al.* 2015;

82 Hightower *et al.* 2015), but fishing times and locations can be managed (Crowder & Murawski
83 1998).

84 Marine bycatch of Atlantic sturgeon occurs in coastal bottom trawl and gillnet fisheries
85 (Stein, Friedland & Sutherland 2004), particularly along the Long Island Coast in the New York
86 Bight (Dunton *et al.* 2015). Summer flounder *Paralichthys dentatus* (Linnaeus, 1766) otter trawl
87 fisheries overlap with sturgeon aggregations, while migration routes within 4.63 km of the coast
88 expose sturgeon to gillnet fisheries generally targeting goosefish *Lophius americanus*
89 (Valenciennes, 1837) (Dunton *et al.* 2010; Dunton *et al.* 2015). Detections of tagged sturgeon at
90 acoustic receivers deployed along coastal Long Island showed broad movements across the
91 region and two primary peaks of occurrence, in late spring and fall during migrations (Dunton
92 2014; Dunton *et al.* 2015). However, variation among receiver stations in the probability of
93 detecting tagged fish, as well as focus on mass detections rather than individual transitions, limit
94 interpretation of movement and survival patterns over time.

95 To better understand seasonal migration patterns along coastal Long Island and variation
96 in weekly mortality, we applied multi-state mark-recapture models (Arnason 1973; Nichols &
97 Kendall 1995; White, Kendall & Barker 2006) to detection data of Atlantic sturgeon tagged with
98 acoustic transmitters. Accounting for time-varying detection probabilities at receiver stations
99 allows time-varying movement rates among stations and time-varying survival rates to be
100 quantified, thereby identifying high mortality periods which should be the focus of conservation
101 efforts. Areas of distribution of sturgeon populations often span hundreds of kilometres of
102 coastline (Dovel & Berggren 1983), but we focus on detailed movements along coastal Long
103 Island at temporal scales directly relevant to the management of fishing activity in which
104 sturgeon are caught incidentally. The research provides the application of acoustic telemetry to
105 estimate ecological rates that can inform spatio-temporal management strategies for species of
106 conservation concern.

107 **Materials and methods**

108 **Study area**

109 The study area is the southern coast of Long Island, New York State, along which Atlantic
110 sturgeon migrate and trawl and gillnet fisheries operate (Fig. 1). The shoreline shifts from north-
111 south to east-west orientation at the mouth of the Hudson River. There is a mean southerly flow
112 of shelf waters down the Mid-Atlantic Bight, with low-salinity water emanating from the Hudson
113 River and Chesapeake and Delaware Bays (Townsend *et al.* 2006). Seasonal changes are strong
114 in the study area, with sea surface temperatures (SST) ranging from 2–25°C (see Fig. S1 in
115 Supporting Information). Seas are typically calmer in summer, and wind speeds increase during
116 fall and winter, deconstructing the summer stratification (Fig. S1).

117 **Fish tagging**

118 Atlantic sturgeon were captured via targeted bottom trawling (Dunton *et al.* 2015). Captured fish
119 were placed into 757 L holding tanks with flowing seawater, underwent standard sampling
120 procedures, and were surgically implanted with ultrasonic transmitters (V16–6H, VEMCO,
121 Bedford, Canada; 69 kHz; high-power output 158 dB re 1uPa @1m; variable transmission delay
122 of either 50–130 s with a 1952 d tag life, or 70–150 s with a 2331 d tag life). All fish were
123 handled under ethical guidelines detailed in National Marine Fisheries Endangered Species
124 Permit #16422 to Stony Brook University. A total of 429 sturgeon were tagged and released over
125 22 field days between May 2010 and April 2012, most in spring or fall (Table 1). Most fish
126 (93%) were released in 2011 or 2012 and most (95%) were released within proximity of station
127 B (Fig. 1; Table 1).

128 All but two tagged fish were detected at some later date following release (Table 1).
129 Tagged sturgeon ranged from 57–181 cm fork length at time of release, corresponding to ages 3–
130 24 (Dunton *et al.* 2016). Genetic analysis of fin clips revealed that 77% of tagged fish were of
131 Hudson River origin and 87.7% were of New York Bight Distinct Population Segment origin
132 (O'Leary *et al.* 2014).

133 **Receiver deployments**

134 Acoustic receivers (VR–2W VEMCO, Bedford, Canada; resonant at 69 kHz) were arranged in
135 'listening lines' perpendicular to shore, designed to detect tagged sturgeon. Receivers were
136 clustered into stations (Fig. 1); each station consisted of one or more lines extending from shore

137 to cover the range of depths at which sturgeon are most commonly found (<20 m; Dunton *et al.*
138 2010). Typically, 8 receivers were deployed in each line beginning 0.5 km from shore and
139 extending offshore approximately 9 km, with adjacent receivers spaced 1.0–1.2 km apart.
140 Receivers were anchored to the seabed at depths ranging from 7–31 m.

141 Movements were accounted for among seven stations (Fig. 1). For relevance to
142 management, primary interest was in movements among stations B–F along coastal Long Island,
143 in areas of active bottom trawling and gillnetting. Stations A and G represented conglomerates of
144 individual receivers deployed southwest and northeast of the main study area, respectively,
145 which provided additional detection data to inform movement and detection estimates at stations
146 B–F. Station A included receivers deployed in the Hudson River and along coasts of New Jersey,
147 Delaware and further south. Station G included receivers deployed in Long Island Sound. Most
148 receivers in these ‘terminal’ stations were deployed by project partners under data sharing
149 agreements. The number of receivers, locations and timing of deployments at terminal stations A
150 and G varied across years and were less consistent than at stations B–F, so a more flexible
151 approach was used for modelling detection probabilities at terminal stations.

152 Receiver station B was operational in years 2010–2013, but other stations C–F along
153 coastal Long Island (Fig. 1) were only operational in 2012–2013. Once deployed, receivers were
154 periodically retrieved to download detection data and then re-deployed for nearly continuous
155 year-round coverage (Table S1). Occasionally individual receivers within a station were lost,
156 yielding a gap along the listening line. We quantified the proportion of coverage at each station
157 over time to incorporate this information as an index of sampling extent in analyses (Melnychuk
158 2009b). Receiver coverage at stations B–F varied over time, usually >75%, but occasionally
159 dropping <50% at some stations for short periods (Fig. S2).

160 **Mark-recapture modelling**

161 Multi-state mark-recapture models (Arnason 1973; Nichols & Kendall 1995; White, Kendall &
162 Barker 2006) were used to quantify detection (p), survival (S) and transition (ψ) probabilities
163 throughout the study period. Transitions are movements among the seven receiver stations A–G,
164 which are treated as mutually-exclusive ‘states’. To provide the temporal resolution desired for
165 addressing management concerns, weekly time steps were used. Parameters for each time step in
166 each stratum were not all freely-varying, however, because the number of parameters that would

167 require estimation over four years and seven strata would be prohibitively large for the sample
168 size available (Burnham *et al.* 1987; Lebreton *et al.* 1992). Instead, constraints were employed to
169 efficiently model changes over time in p , S and ψ parameters while still allowing for weekly time
170 steps. Constraints involved annual or seasonal pooling of parameters as well as pooling
171 parameters among strata. In other words, we sought a desirable balance between model
172 complexity for biological realism and model simplicity to avoid over-fitted models or poorly-
173 estimated coefficients (Appendix S1).

174 To quantify seasonal migration patterns, we associated weekly time steps with four
175 seasons in each year: we considered 16 time steps for spring (1 March–20 June), 10 time steps
176 for summer (21 June–29 Aug.), 10 time steps for fall (30 Aug.–7 Nov.) and 16 time steps for
177 winter (8 Nov.–28/29 Feb.). For parsimony, pooling detection, survival and transition probability
178 parameters by season was necessary in some models.

179 Detailed approaches and assumptions used for mark-recapture modelling are described in
180 Appendix S1. Briefly, we constructed detection histories of individual tagged sturgeon at stations
181 A–G and used these as input data to fit multinomial regression models containing parameters for
182 survival, transition and detection probabilities over time. Environmental data were incorporated
183 as covariates for estimating model parameters. Three survival sub-models, four movement sub-
184 models and four detection sub-models were hypothesized; the resulting combinations of 48
185 candidate models were compared using formal model selection methods (Table S2). For the best
186 two models, body size effects on survival and movement probabilities were evaluated (Table
187 S3). Mark-recapture analyses sourced Program MARK (White & Burnham 1999) through the R
188 package RMark (Laake 2013).

189 **Results**

190 Model selection procedures showed strong support for four models within 1.0 AICc units of one
191 another (Appendix S1; Table S3). These models include effects of season, SST and body size on
192 transition probabilities (ψ), and effects of three environmental covariates (wind speed, wave
193 height and SST) and receiver coverage on detection probabilities (p). Survival probabilities (S) in
194 these four models are influenced by either SST or a categorical season effect, and influenced or
195 not by fork length (Table S3). Results presented below are based on the AICc-preferred model

196 [$S.3_{FL}, p.4, \psi.4_{FL}$] (Table S4), and alternate results are shown for model [$S.2, p.4, \psi.4_{FL}$] (Table
197 S5). General conclusions are consistent across the top four models.

198 **Survival patterns**

199 Survival probability estimates for weekly time steps t , \hat{S}_t , ranged from 97.06–99.98% over the
200 duration of the study, with an annual geometric mean of 99.76% (Fig. 2). These imply average
201 annual survival rates of 88.27% (SE 0.45%) under model [$S.3_{FL}, p.4, \psi.4_{FL}$]. Weekly \hat{S}_t tended
202 to be lowest in spring (99.44%, SE 0.15%), intermediate in summer (99.74%, SE 0.01%) and
203 highest in fall (99.89%, SE 0.01%) and winter (99.88%, SE 0.01%) (Fig. 2a). Weekly S_t were
204 not freely-varying, they were constrained as functions of SST_t and change in sea surface
205 temperature, $\Delta SST_{t-1 \rightarrow t}$. The effect of $\Delta SST_{t-1 \rightarrow t}$ on S_t was greater than the effect of SST_t (Fig. 3;
206 Table S4). During weeks of rapidly increasing temperatures, \hat{S}_t were lowest, and were greatest
207 during weeks of decreasing temperatures (Figs 2 & 3). Model [$S.2, p.4, \psi.4_{FL}$] showed similar
208 results: weekly \hat{S}_t of 99.64% (spring), 99.54% (summer), 99.93% (fall), and 99.91% (winter)
209 (Fig. 2b); annual geometric mean weekly survival, 99.76%; and average annual survival,
210 88.22%.

211 A slight negative effect of fork length on S was observed. Smaller fish enjoyed a slight
212 survival advantage ($\beta_{FL} = -0.0094$, SE 0.0053), but 95% confidence limits did not exclude zero
213 (Table S4).

214 **Movement patterns**

215 Seasonal movements among detection strata were not unidirectional along coastal Long Island,
216 they involved complex patterns. In spring, southwestward movements were more common than
217 northeastward movements (Figs 4, S4 & S5). In summer, Atlantic sturgeon were uncommon
218 along coastal Long Island (Fig. S3) and little movement occurred among strata as shown by the
219 predominant intra-stratum loops in Fig. 4 (indicating a lack of transition to different strata in
220 successive time steps; Fig. S6). In fall, weekly movements were slightly more frequent in both
221 directions than in summer. In winter, sturgeon showed strong directional movement
222 northeastward.

223 Movement probabilities among strata, $\psi^{stratum \rightarrow stratum}$, were modelled with constraints of
224 separation distance between pairs of receiver stations (Fig. S7). Separation distance had similar
225 effects for southwestward and northeastward movements, with transitions being more frequent
226 among strata that were closer together (Fig. 5; Table S4).

227 Movements over time, $\psi_{t \rightarrow t+1}$, were modelled with constraints of season, SST_t and $\Delta SST_{t-1 \rightarrow t}$.
228 Northeastward ψ were greater when SST_t was lower, while southwestward ψ showed little
229 effect of SST_t *per se* on movements (Fig. 5). Instead, southwestward ψ were positively related to
230 $\Delta SST_{t-1 \rightarrow t}$, with southwestward movements more common during periods of increasing
231 temperature (Fig. 5). The interaction between SST_t and $\Delta SST_{t-1 \rightarrow t}$ on $\psi_{t \rightarrow t+1}$ was also positive for
232 southwestward movements (Table S4), suggesting a greater tendency for southwestward
233 movement when temperatures were both high and increasing.

234 There was a strong positive effect of body size on overall ψ ($\beta_{FL} = 0.0065$, SE 0.0010).
235 Atlantic sturgeon with longer fork lengths at time of tagging were more likely to move among
236 strata in successive time steps (Tables S3 & S4).

237 **Detection probabilities**

238 Estimates \hat{p} varied greatly among strata and seasons. For the aggregate stations A and G,
239 inconsistencies in the number and location of receivers deployed across years and seasons
240 required flexibility in modelling p , and indeed there was considerable variation in \hat{p} at these
241 terminal stations, especially in the first two years of the study (Fig. S8). In these years, fewer
242 tagged fish and fewer deployed receivers led to large seasonal changes and large uncertainties in
243 \hat{p} at station A, but in the last two years \hat{p} were typically higher and estimated with greater
244 precision. Detections were less frequent at station G, so the relationship between p and SST was
245 constrained to be common across years, whereas relationships between p and SST were allowed
246 to vary among years at station A (Fig. S8).

247 Along coastal Long Island, \hat{p} were typically <40% for stations C–E, <10% for station F
248 and ranged widely over time from 20–90% at station B (Fig. S8). The variability in \hat{p} over time
249 at stations B–F was captured by variability over time in receiver coverage and environmental
250 covariates. As expected, greater p was associated with greater receiver coverage (Fig. S9).
251 Influences of wind speed, wave height and SST on p were complex. Strong support was found for

252 all three 2-way interactions on p , with negative $\beta_{wind:wave}^{B-F}$, positive $\beta_{wind:SST}^{B-F}$ and positive $\beta_{wave:SST}^{B-F}$
253 effects observed. This implied that the overall positive effect of wave height on p was mediated
254 by the interactions such that it lessened if both wave height and wind speed increased, and
255 increased if both wave height and SST increased. This resulted in \hat{p} tending to be greatest at
256 intermediate levels of wind speed, wave height and SST (Fig. S9).

257 Discussion

258 Atlantic sturgeon use the Long Island Coast as a migration corridor, displaying strong seasonal
259 patterns with peak occurrences in spring and fall. The few weeks during late spring of lowest
260 survival may be a particularly sensitive time for sturgeon with respect to fishing activity, as they
261 coincide with otter bottom trawl and gillnet fishing effort (Dunton *et al.* 2015). Although
262 sturgeon are not targeted directly, incidental catch likely contributes to the high total mortality
263 observed in late spring (Fig. 6). Causes of mortality were not directly observed with acoustic
264 telemetry, but understanding the spatial extent and timing of mortality can aid in developing
265 management strategies to increase sturgeon survival. Such mortality patterns can be assessed
266 through real-time monitoring programs.

267 Population recovery

268 Atlantic sturgeon are long-lived and not typically able to withstand high fishing mortality
269 (Musick 1999). Natural mortality has been estimated at $M = 0.07$ based on a life-history-
270 invariant relationship with assumed 60-year longevity (ASMFC 1998; Kahnle, Hattala &
271 McKown 2007). An acceptable fishing rate, defined as half the virgin level of eggs-per-recruit,
272 was estimated at $F_{50\%} = 0.03$ for fully-recruited individuals (ASMFC 1998; Kahnle, Hattala &
273 McKown 2007). Additionally, population projections predict that 6% total annual mortality
274 would put recovering populations at risk (ASMFC 2007). Approximately 6% cumulative
275 mortality was estimated for tagged sub-adult sturgeon during relatively short periods of 12–17
276 weeks in late spring (Fig. 6), and total annual mortality estimates were twice this level (11.7%).
277 The body size range for which mortality thresholds of fully-recruited sturgeon were estimated
278 does not completely overlap with that of sub-adult migrants telemetered in this study, but the
279 high mortality estimated in this study is nonetheless concerning. Rates of tag loss and tag-related

280 mortality have not been well-studied for this endangered species, but are likely low given the
281 surgical implantation of tags and the relatively low tag:body mass ratio compared to other fish
282 telemetry studies. If mortality along coastal Long Island is greater than typical levels along the
283 greater Atlantic Coast and Hudson River, and if our study period is representative of longer-term
284 trends, then annual total mortality of the Hudson River population is presently too high to allow
285 for recovery. This is consistent with Atlantic sturgeon populations further south, for which
286 annual mortality is considered sufficient to hinder recovery (Hightower *et al.* 2015).

287 The weak relationship between body size and total survival was in the opposite direction
288 than expected and is suggestive of size-selective bycatch mortality. Variability in natural
289 mortality due to body size is common in marine fishes (Lorenzen 1996), with larger fish
290 enjoying a size advantage, but in this study survival was slightly greater for smaller fish. As total
291 mortality is comprised of both natural and fishing mortality, the unexpected pattern observed for
292 total mortality may result from either greater selectivity for larger individuals in incidental
293 fisheries or a higher mortality rate of discarded bycatch for larger individuals, potentially
294 outweighing any opposite pattern for natural mortality. Size distributions of sturgeon bycatch are
295 dome-shaped (Dunton *et al.* 2015), and body sizes of sturgeon tagged in this study were mostly
296 in the lower portion of these distributions, within the region of positive slope in which larger
297 individuals account for more bycatch than smaller individuals. This provides support for size-
298 selective fishing mortality (and thus considerable overall fishing mortality) in fisheries that catch
299 sturgeon incidentally.

300 Seasonal survival estimates can be used to approximate the reduction in annual mortality
301 that could be achieved if seasonal closures were implemented in the state waters of New York
302 during the spring peak in occurrence (April–June). Sturgeon bycatch in trawl and gillnet fisheries
303 is relatively high in spring and summer months along coastal Long Island (Dunton *et al.* 2015).
304 Assuming that the estimated average weekly mortality in fall and winter of 0.12% is comprised
305 entirely of natural mortality, and applying this weekly mortality to a full year, yields annual
306 natural mortality of 5.88%. The difference between annual total mortality, 11.73%, and annual
307 natural mortality results in estimated annual fishing mortality of 5.86%, attributable to incidental
308 catches. If the assumption that fall and winter mortality is comprised of only natural mortality is
309 incorrect, and instead bycatch mortality occurs throughout the year, the estimate of annual
310 fishing mortality would be even greater.

311 **Seasonal movements**

312 Atlantic sturgeon movement and survival patterns varied with *SST* in complex ways.
313 Northeastward movements were associated with low temperature periods in winter, when weekly
314 survival was high. The scarcity of detected sturgeon along coastal Long Island in summer did not
315 result from lower *p* in summer (Fig. S8), but instead reflected lower occurrence (Fig. S3). In
316 spring, during the greatest weekly increases in *SST*, weekly survival was low and southwestward
317 movements along the coast (often into the Hudson River) were frequent. It is unknown whether
318 sturgeon directly respond to low temperature (in winter) or rapidly increasing temperature (in
319 spring) by increasing movement rates northeastward or southwestward, respectively, or whether
320 temperature is simply correlated with other seasonally-changing factors. Whether the
321 behavioural response is to temperature or to other temperature-related factors, it appears to have
322 survival consequences. The relationship with temperature offers opportunities for implementing
323 spatio-temporal fishery closures during spring migration periods but then relaxing restrictions in
324 summer months, consistent with sturgeon movements (Breece *et al.* 2016; Dunn *et al.* 2016).

325 Individual and population characteristics also affected sturgeon migration behaviour. The
326 observed influence of body size on movement rates is not surprising, as larger fish are typically
327 stronger swimmers than smaller fish during migration periods. There is also some indication of
328 differential migration behaviour among individuals within the Hudson River (Dunton 2014).
329 Notably, conclusions regarding direction of movement along coastal New York depend on the
330 geographic scale considered. Limiting focus to only stations B–F along coastal Long Island
331 revealed northeastward spring migrations and southwestward fall migrations (Dunton 2014),
332 whereas the larger area considered in the present study revealed the opposite pattern, driven
333 largely by spring movements into the Hudson River (part of station A) and fall movements out of
334 the river. Although tagged fish were primarily of Hudson River origin, fish from other
335 populations also migrate along the New York coast (Dunton *et al.* 2012; Wirgin *et al.* 2015).
336 These findings together suggest a diversity of migration behaviours both among individuals and
337 among populations. Future research is needed to relate migration behaviour to genetic origin and
338 compare survival between alternate migration routes.

339 **Modelling considerations**

340 An appropriate balance between biological realism and statistical robustness (e.g. avoidance of
341 over-fitting a model to sparse data) is often challenging in mark-recapture modelling. In multi-
342 state models, complexity increases non-linearly and general models (in which separate
343 parameters are estimated for each stratum and each time step) become prohibitive for modest
344 sample sizes (Nichols & Kendall 1995; White, Kendall & Barker 2006). The candidate models
345 we considered were highly constrained. Time steps were weekly, but in no sub-models were
346 there unique parameters estimated for individual weeks. Parameters were instead constrained to
347 be common across time steps within a season or to be functions of environmental covariates.
348 Similarly, movements among strata were constrained to be functions of environmental covariates
349 and the separation distance between pairs of strata. This approach permitted a high temporal
350 resolution of movement and survival parameters without having models become too complex for
351 the sample size of tagged fish (Melnychuk 2009a). For survival, near-equivalent support was
352 found for temperature-constrained and categorical seasonal effects, and only slight body size
353 effects were observed, but annual survival rates as well as weekly detection and transition
354 probabilities were similar across the top four candidate models.

355 The study lasted four years, but sample size of tagged fish and sampling effort by
356 receivers were greater in 2012–2013. Survival and movement sub-models did not involve any
357 year-specific effects, so estimates for 2010–2011 are heavily weighted towards detection data
358 from 2012–2013. Detection probability sub-models, however, did involve year-specific effects,
359 designed to capture the change in sampling effort between the first two and last two years. Most
360 sturgeon were tagged and released near station B, but the study was long enough to ensure
361 sufficient mixing among stations following release dates (97.6% of sturgeon released near station
362 B were later detected at a different station). Releases were also spread out over several dates
363 which further aided in mixing and ensuring that observed patterns of tagged fish are likely
364 representative of the population and its seasonal movements.

365 The spatial focus of this study was the Long Island Coast, involving strata B–F; receiver
366 stations were purposefully placed in areas of active trawling and gillnetting to quantify
367 movement and survival patterns. Terminal strata A and G were outside this area and are of less
368 management interest for the present study, but they provided detection data which informed
369 movement estimates within coastal Long Island. Because strata A and G were aggregations of
370 receivers over wide geographic areas, the strong tendencies of staying within stratum A or

371 stratum G in successive time steps (loops in Fig. 4) do not imply that tagged fish were not
372 moving frequently, rapidly, or great distances within these terminal strata. Future analyses
373 involving migration patterns along the entire Atlantic coast could identify whether mortality
374 patterns change when shifting focus from a regional to a coastwide scale.

375 **Planning of spatio-temporal fishery closures**

376 Conservation efforts targeted at reducing sturgeon bycatch in coastal New York could increase
377 survival of the Hudson River population in particular, and other populations to some extent,
378 thereby helping to reverse abundance declines. Protection from marine bycatch during
379 occupation of the Hudson River, and *de facto* protection provided in many states by trawling
380 limitations, leaves New York and Connecticut coastal waters lacking protection from
381 commercial fisheries during Atlantic sturgeon migrations (Dunton *et al.* 2010). The higher
382 estimated mortality rates in late spring compared with other seasons likely result from bycatch of
383 bottom trawl and gillnet fisheries along coastal Long Island (Dunton *et al.* 2015). Implementing
384 fishery closures during this critical period in this region would seem promising for decreasing
385 bycatch mortality of the Hudson River population (Crowder & Murawski 1998; Neat *et al.* 2014;
386 Dunn *et al.* 2016).

387 The period of late spring and the region of coastal Long Island are shorter and smaller
388 than annual time scales and the full area of population distribution, respectively, but
389 socioeconomic considerations still preclude fishery closures over this full period and region.
390 More plausibly, closures could involve specific weeks and locations along coastal Long Island.
391 To assist with in-season predictions of critical times, the observed non-linear influence of change
392 in *SST* on sturgeon survival can be used. Lowest survival occurred as temperatures rose quickly;
393 if particularly low survival can be avoided by reducing fishing activity during weeks of rapid
394 temperature increase (e.g. >1.5 or $2\text{ }^{\circ}\text{C}\cdot\text{week}^{-1}$), this could increase overall annual survival more
395 than actions targeted at other times of year. The specific, weekly-resolution timing of *SST*
396 increase during late spring varies among years (Fig. S1), and temperature data collected from
397 weather and oceanographic buoys along coastal New York can be used in real time to predict the
398 movement and presence of sturgeon in potential fishing locations. Additionally, some acoustic
399 receivers can remotely communicate detections of tagged sturgeon, which could also inform the
400 implementation of fine-scale spatio-temporal closures when sturgeon become locally abundant.

401 Such real-time observations have the potential to restrict in-season fishery closures to the times
402 and locations of highest bycatch risk while allowing continued local fishing activity in times and
403 locations of lower bycatch risk. Atlantic sturgeon could thus become an example of using
404 acoustic telemetry and remote sensing technologies to reduce non-intentional mortality of a long-
405 lived migratory species with endangered status to promote population recovery.

406 **Application of acoustic telemetry to conservation**

407 Acoustic telemetry was effective in meeting study objectives—to estimate seasonal movements
408 and mortality of Atlantic sturgeon, and to identify critical periods and areas which conservation
409 actions may target—and has advantages over traditional recapture methods. Acoustic tags
410 allowed repeated detections in multiple locations, providing more information per tagged
411 individual than a single location and time of recapture typically provided by traditional methods;
412 increased information gain is essential for the limited sample sizes typically used in research of
413 endangered or depleted species. Repeated detections across widespread locations allowed for
414 weekly resolution of mortality estimates, and at the same time allowed for quantifying broader
415 movement and survival patterns across years and throughout the region. Traditional mark-
416 recapture methods would not achieve these simultaneous levels of resolution without unrealistic
417 tag numbers and levels of tag recovery effort. Traditional methods also rely on tags being
418 returned by fishers; reporting rates in some fisheries may be low, inconsistent, poorly estimated,
419 and potentially biased against areas and times of high bycatch that could trigger fishery closures
420 (Brownie *et al.* 1985). A well-designed network of local acoustic telemetry studies can provide
421 large-scale monitoring opportunities to inform regional conservation strategies while
422 simultaneously providing high-resolution movement and mortality patterns to identify localized
423 threats. Future research is needed to evaluate alternative (or complementary) approaches for
424 avoiding incidental catch—such as move-on rules (Dunn *et al.* 2014), gear alteration, and tow-
425 length reduction—in terms of research cost, lost fishery revenue, and efficacy of bycatch
426 reduction. As acoustic telemetry technology becomes more widely adopted in marine and
427 freshwater systems, it has the potential to address applied ecological questions at multiple spatial
428 and temporal scales relevant to management and conservation concerns.

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438 Atlantic Sturgeon outside of our study area.

439 **Data accessibility**

440 Sequences of detection histories of individual tags used in this study as input data for multi-state
441 mark-recapture models are available in the Knowledge Network for Biocomplexity online data
442 repository (Melnychuk, 2016). In the file, ‘Melnychuk_etal_JApplEcol_inputData.txt’, each digit
443 of ‘ch’ represents a weekly time step. The first letter A–G in the sequence represents release, and
444 all remaining letters A–G represent detection at stations A–G within the time step. Zeros
445 following release indicate time steps of no detections, and zeros preceding release are used to
446 align the differing release dates across tagged fish. Tags, ‘tag’, are numbered T1–T426, Dates on
447 which individual fish were tagged and released, ‘relDate’, are given. Fork lengths, ‘FL’, are
448 given in cm.

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554
 555

556 **Tables**

557 Table 1. Release times, numbers and body sizes of tagged Atlantic sturgeon throughout the study
 558 period

Release date	Number released	Number detected thereafter	Nearest station to release *	FL mean \pm SD (cm) †	Range FL (cm) †
2010-05-18	3	3	B	76.0 \pm 0.5	75.5-76.5
2010-05-19	9	9	B	91.9 \pm 14.3	72.0-109.0
2010-06-14	8	8	B	104.4 \pm 8.5	94.5-122.0
2010-06-15	4	4	B	117.2 \pm 12.0	105.0-130.0
2010-10-23	1	1	A	104.0	-
2010-10-25	3	3	A	137.2 \pm 38.4	103.5-179.0
2011-04-13	2	2	A	65.9 \pm 12.2	57.2-74.5
2011-04-14	3	3	A	66.7 \pm 3.4	64.2-70.6
2011-04-25	1	1	A	59.6	-
2011-04-26	4	4	A	73.6 \pm 8.7	65.1-83.7
2011-04-27	4	4	A	72.8 \pm 7.3	64.5-82.0
2011-05-24	68 ‡	67 ‡	B	114.6 \pm 14.8 ‡	76.7-155.0 ‡
2011-08-11	47	47	B	112.5 \pm 16.0	75.6-138.3
2011-09-11	40	40	B	103.2 \pm 19.1	71.9-164.0
2011-10-11	26	26	B	101.0 \pm 17.3	77.3-127.0

2011-10-13	1	1	B	121.0	–
2011-10-24	1	1	A	133.5	–
2011-10-31	60	60	B	110.7±18.1	73.7–181.0
2011-12-10	2	2	B	121.6±3.2	119.3–123.8
2012-02-05	46	46	B	91.7±12.1	72.5–127.9
2012-03-05	74	73	B	101.4±18.0	76.0–149.6
2012-04-05	22	22	B	102.9±24.4	71.6–178.5
Total	429 ‡	427 ‡	A: 20 B: 409	104.4±19.7	57.2–181.0

559

560 * See labels in Fig. 1.

561 † Fork length (FL) summary statistics for released fish; SD = standard deviation.

562 ‡ Three fish from 2011-05-24 release group either died or had tags extruded near station B
563 shortly after release and were detected continuously thereafter. These fish were excluded from
564 analyses resulting in n=426, of which 424 were detected thereafter.

565 Figure Captions

566

567 Figure 1. Map of study area. Dark circles show acoustic receivers maintained by Stony Brook
568 University; lighter circles show receivers maintained by Atlantic Cooperating Telemetry
569 Network partners where Atlantic sturgeon were commonly detected. Receiver stations A–G were
570 treated as distinct states in multi-state models: A, all areas south and west of B including Hudson
571 River (area shaded); B, Rockaway Peninsula and Sandy Hook Spit (area shaded); C, Jones
572 Beach; D, Fire Island; E, Shinnecock; F, Montauk Point; G, all areas north and east of F
573 including Long Island Sound (area shaded). Major water bodies and two-letter state
574 abbreviations are labelled. Inset shows U.S. mid-Atlantic coast, with dashed box showing main
575 study area. Scale bar applies to main map.

576

577 Figure 2. Weekly Atlantic sturgeon survival probability estimates under (a) model $[S.3_{FL}, p.4, \psi.4_{FL}]$
578 and (b) model $[S.2, p.4, \psi.4_{FL}]$, with 95% confidence intervals. Average weekly sea

579 surface temperature (*SST*, °C) measured at the New York Harbor Entrance Buoy is overlaid in
580 (a); one period of four time steps had no available *SST* data, during which *SST* values were
581 linearly interpolated. Seasons are shown with grey shading: spring = lightest; winter = darkest.
582 Primary vertical axis does not begin at 0.

583
584 Figure 3. Effects of sea surface temperature (*SST*, °C), change in *SST* between successive time
585 steps (ΔSST) and their interaction on survival probability estimates. Solid lines show partial
586 survival predictions, with lower 95% confidence band (dashed). Vertical axes do not begin at 0.

587
588 Figure 4. Seasonal transition probabilities among strata. Estimated transition probabilities for
589 each time step are averaged across each season, separately for each of 49 possible transitions.
590 Season durations are: spring, 1 March–20 June; summer, 21 June–29 Aug.; fall, 30 Aug.–7 Nov.;
591 winter, 8 Nov.–28/29 Feb. Northeastward transitions are shown by arches above station labels,
592 southwestward transitions are shown by arches below station labels, and lack of movement to
593 different strata in successive time steps is shown by loops adjacent to station labels. Average
594 transition probabilities into each stratum and from each stratum sum to 1, with line thicknesses
595 proportional to these 0–1 probabilities.

596
597 Figure 5. Effects of separation distance between receiver stations, sea surface temperature (*SST*,
598 °C), change in *SST* between successive time steps (ΔSST) and interaction of *SST* and ΔSST on
599 transition probability estimates. Estimates are shown only for movements involving stratum D,
600 for clarity. Partial survival predictions (solid line) and 95% confidence bands (dashed) are
601 shown.

602
603 Figure 6. Cumulative mortality during periods when tagged Atlantic sturgeon were frequently
604 detected at one or more stations B–F in the final two years of the study. Selected intervals are
605 arbitrary, chosen to correspond to periods of greatest numbers detected (2012-03-01 to 2012-06-
606 21; 2012-08-30 to 2012-12-20 and 2013-04-26 to 2012-07-12). Cumulative mortality is
607 calculated as 100% minus the product of weekly survival estimates during the interval.

608 **Supporting Information**

609 Additional Supporting Information may be found in the online version of this article.

610 **Appendix S1.** Detailed methods for mark-recapture modelling approaches.

611 **Table S1.** Number and duration of acoustic receiver deployments at stations B–F throughout the
612 study period.

613 **Table S2.** Initial information-theoretic comparison of candidate mark-recapture models.

614 **Table S3.** Final information-theoretic comparison of mark-recapture models involving possible
615 effects of body size on survival and transition probabilities.

616 **Table S4.** Estimated coefficients for AICc-best model [$S.3_{FL}$, $p.4$, $\psi.4_{FL}$].

617 **Table S5.** Estimated coefficients for model [$S.2$, $p.4$, $\psi.4_{FL}$].

618 **Fig. S1.** Time series of wind speed, wave height and sea surface temperature throughout the
619 study period.

620 **Fig. S2.** Index of detection coverage by weekly time step for detection stations B–F.

621 **Fig. S3.** Number of tagged fish detected per day at stations during the study period.

622 **Fig. S4.** Estimated transition probabilities for northeastward movements along the Long Island
623 Coast.

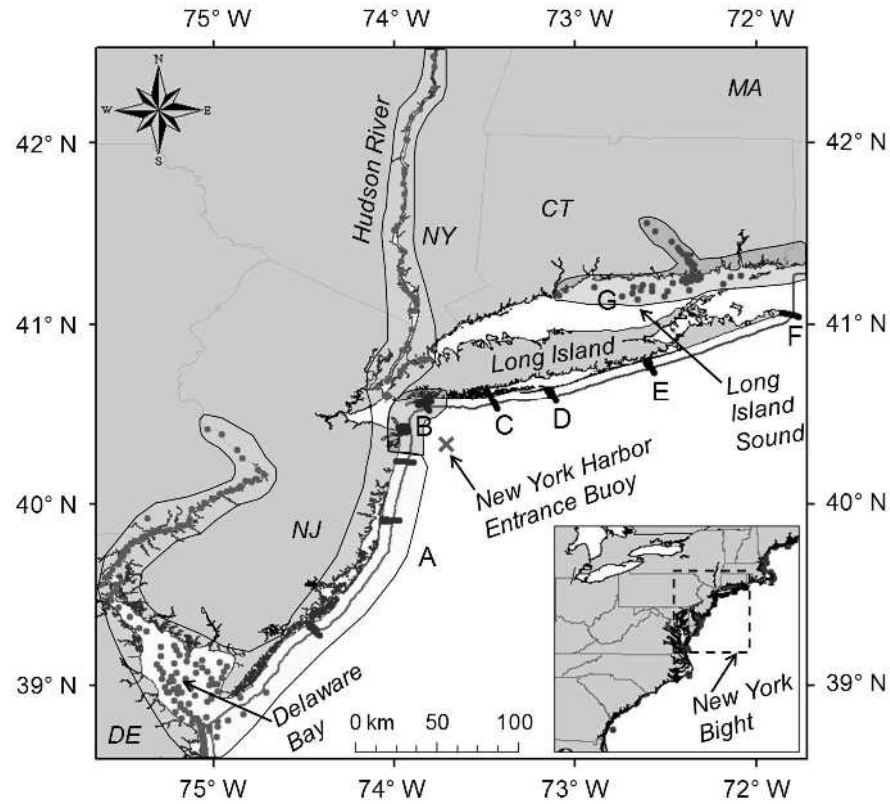
624 **Fig. S5.** Estimated transition probabilities for southwestward movements along the Long Island
625 Coast.

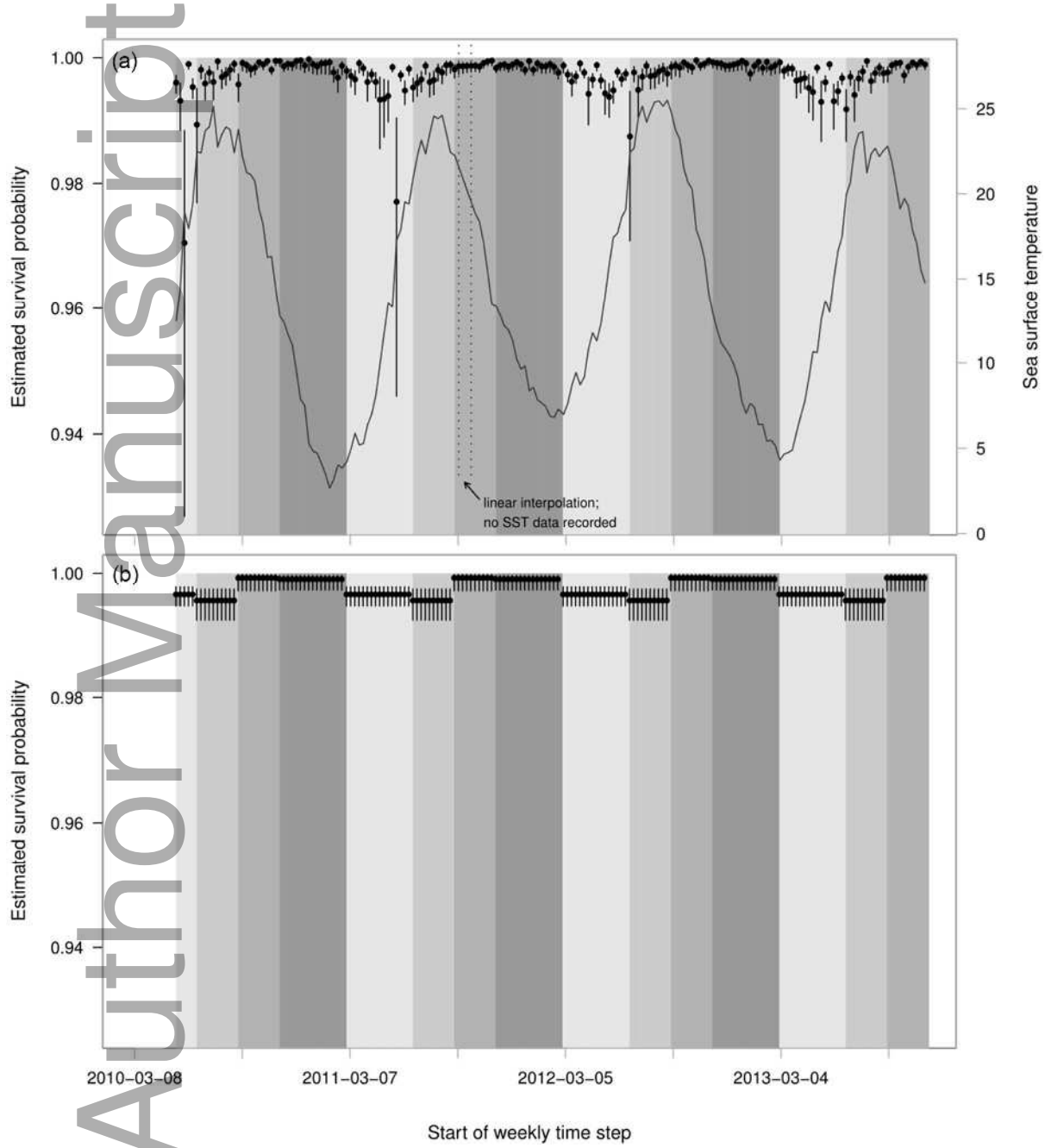
626 **Fig. S6.** Implied transition probabilities for remaining in the same stratum between successive
627 time steps.

628 **Fig. S7.** Matrix of separation distances between pairs of strata.

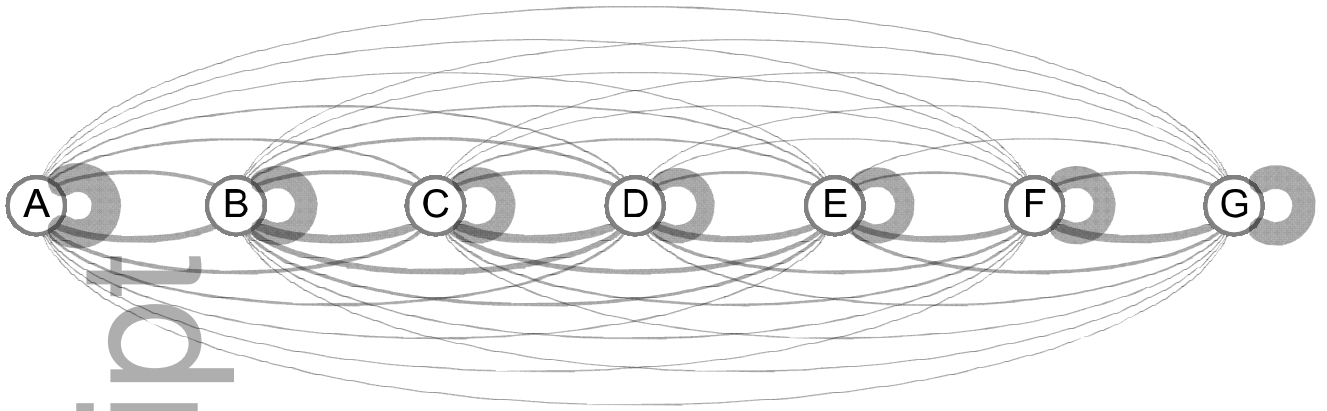
629 **Fig. S8.** Estimated detection probabilities at stations A–G.

630 **Fig. S9.** Effects of wind speed ($\text{m}\cdot\text{s}^{-1}$), wave height (m), sea surface temperature (SST , $^{\circ}\text{C}$), 2-
631 way interactions among them and receiver coverage on estimated detection probabilities.

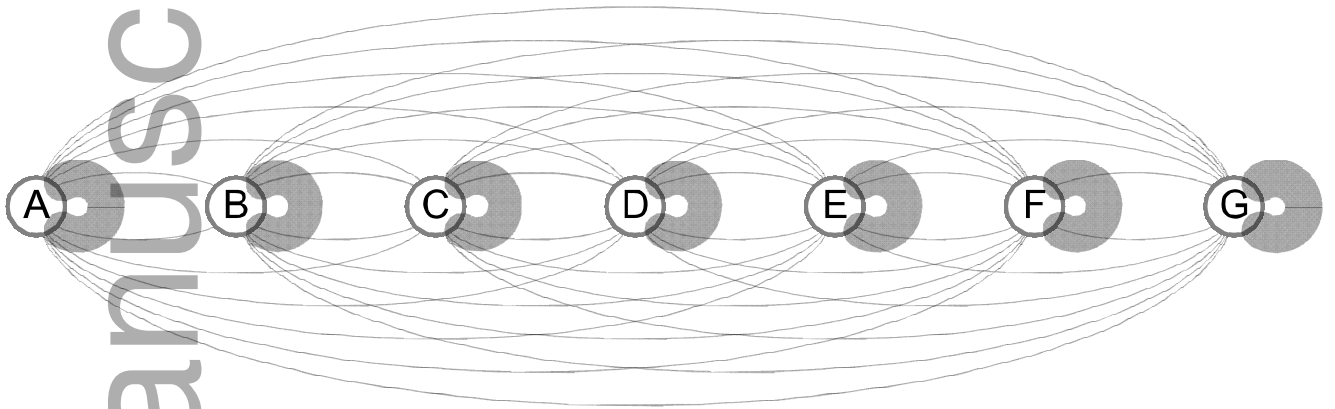




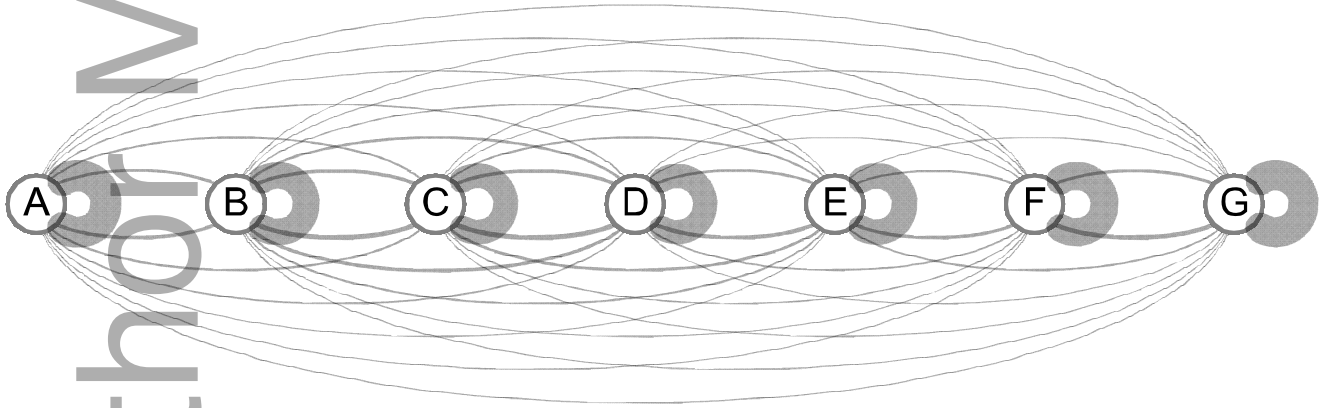
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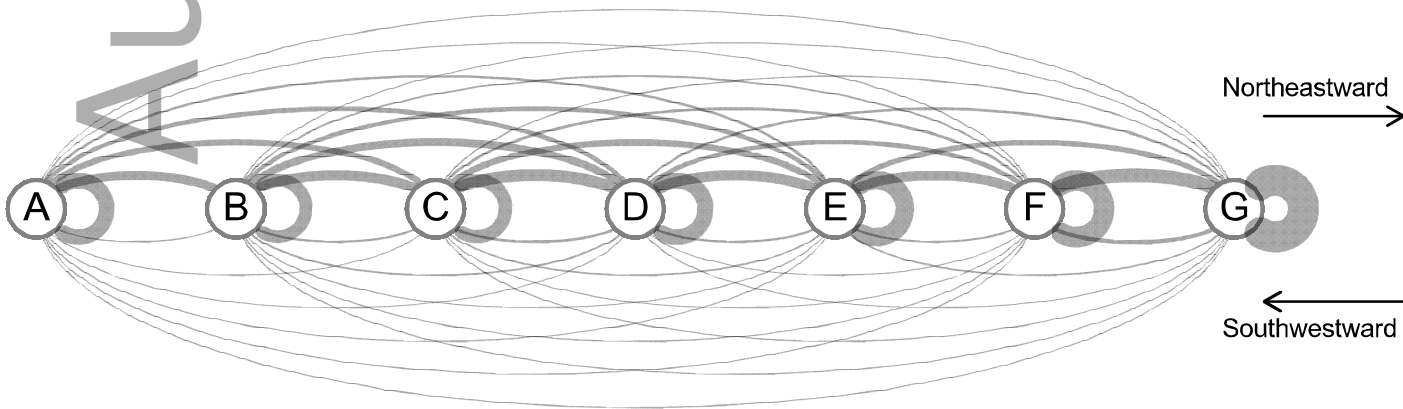
Summer

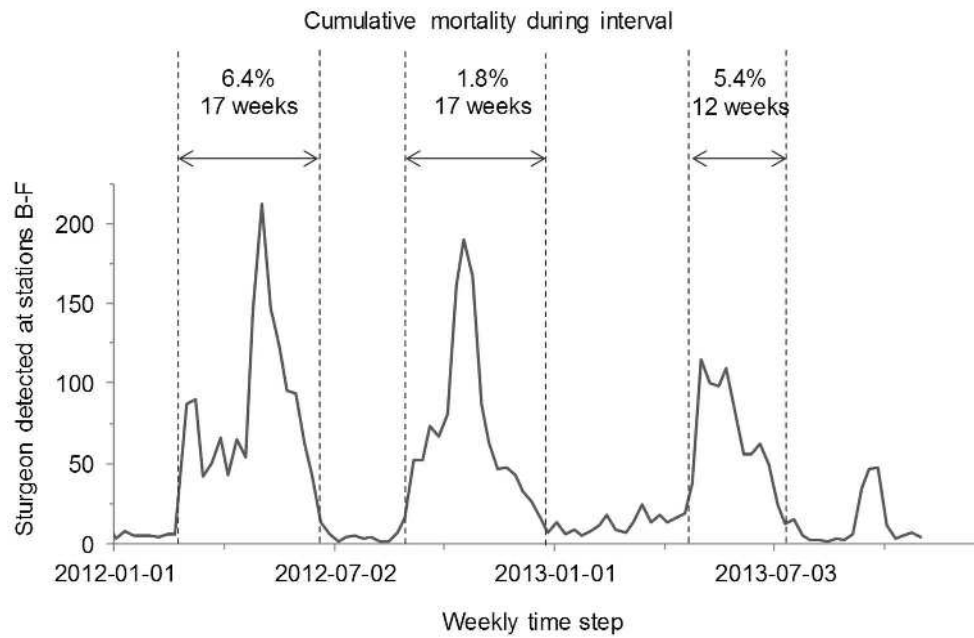


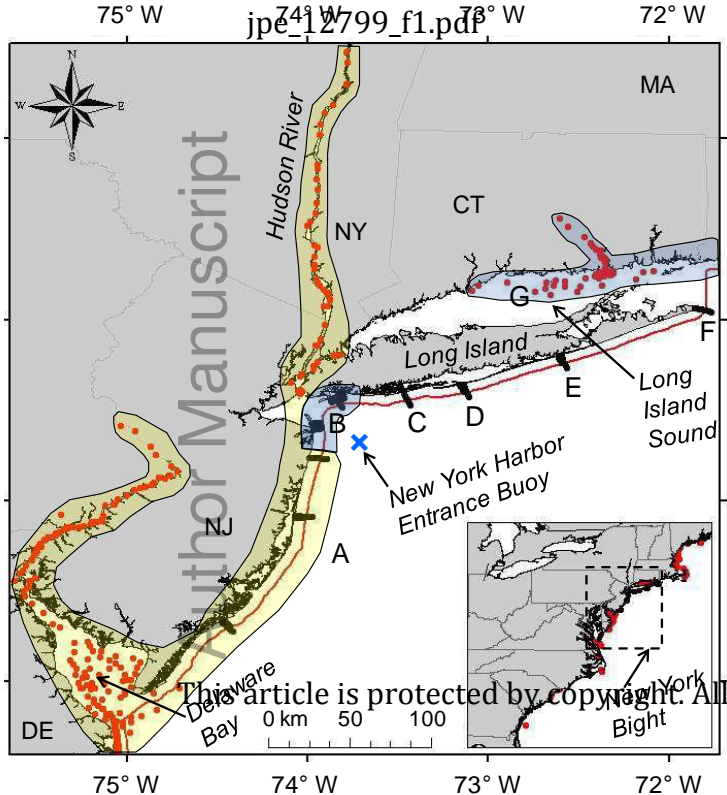
Fall

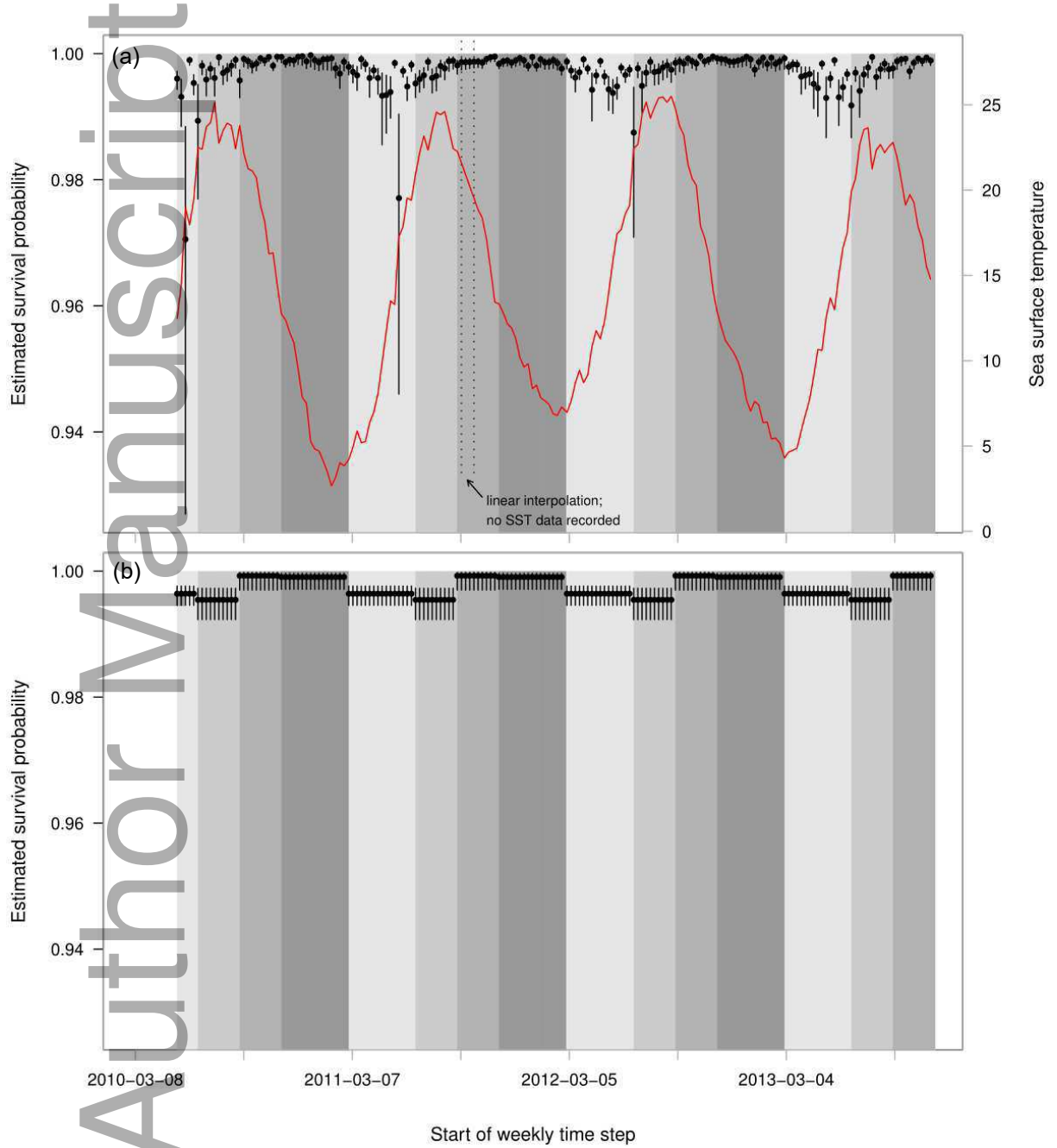


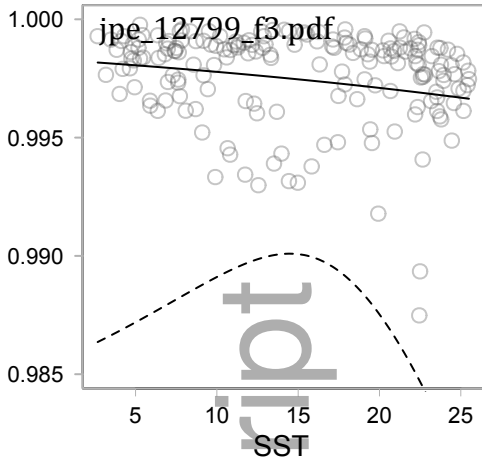
Winter



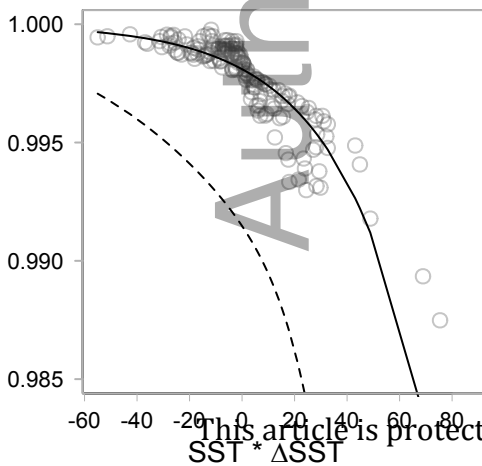
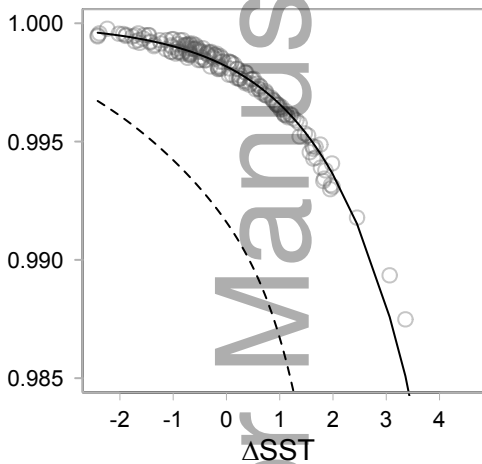






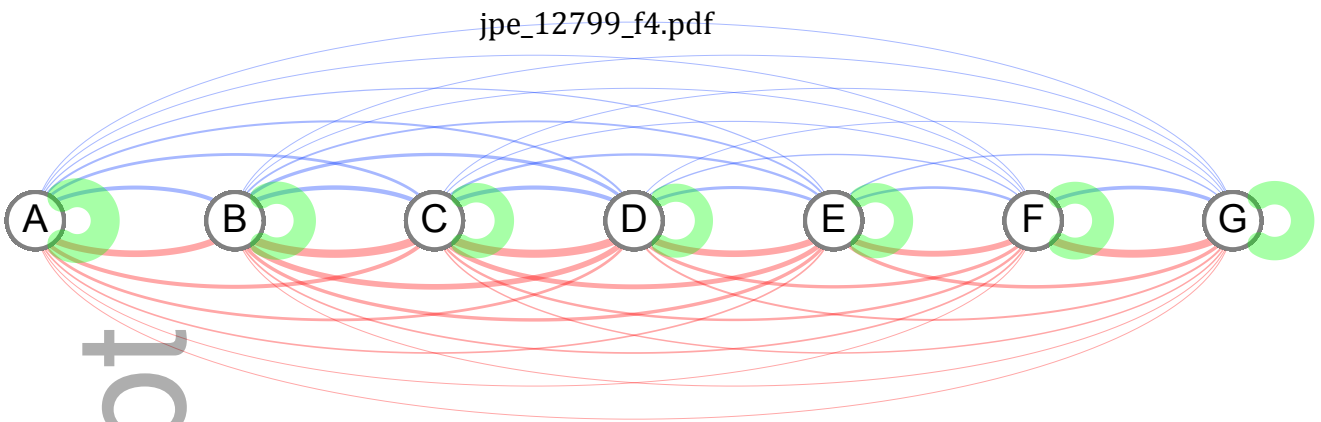


Estimated survival probability

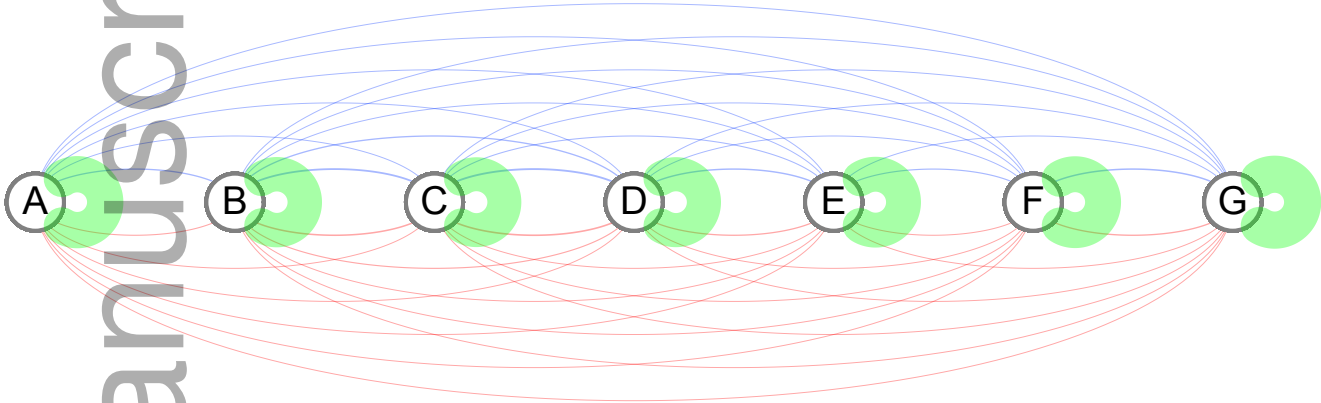


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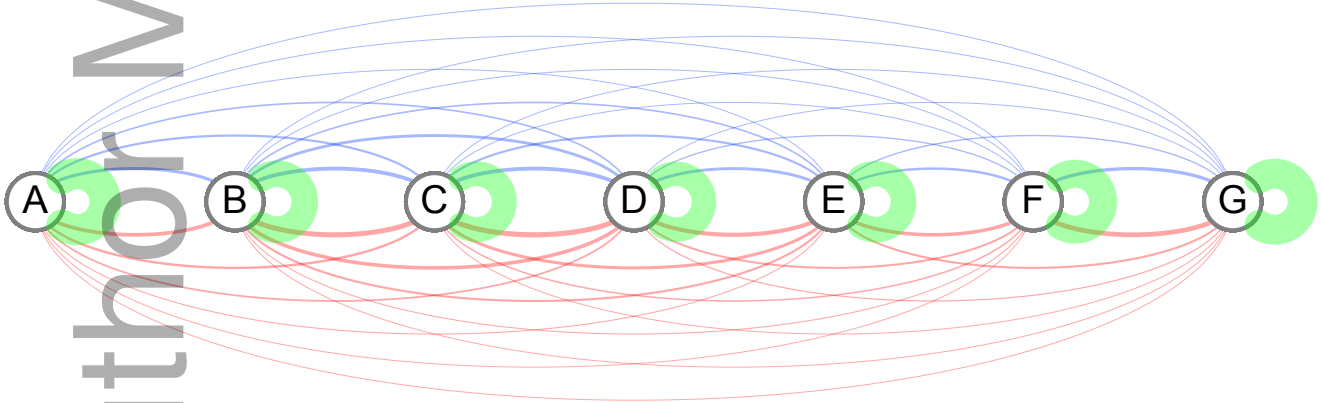
Spring



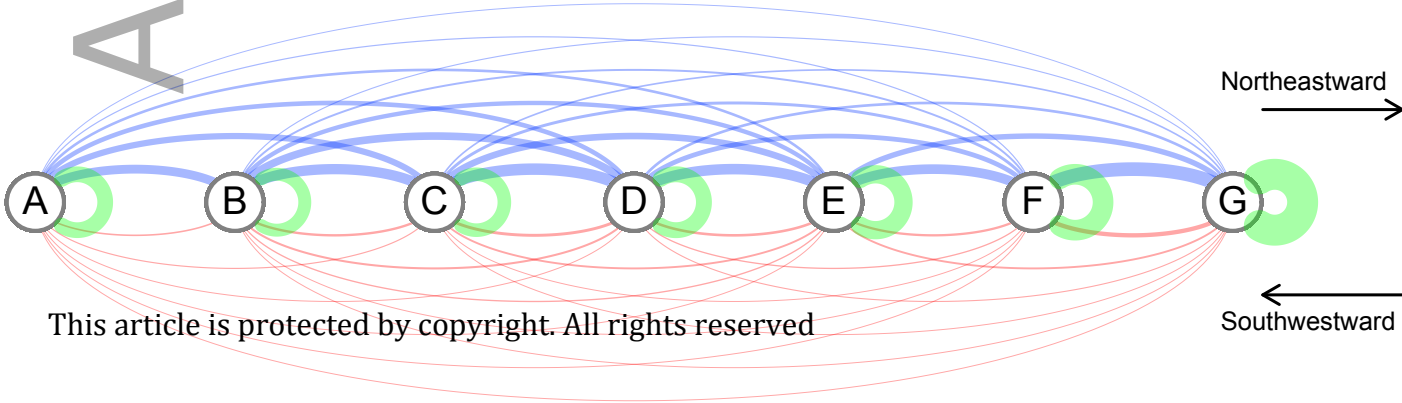
Summer



Fall



Winter



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Estimated transition probability

