

1 **Intraspecific variation in migration timing of green sturgeon in the**  
2 **Sacramento River system**

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26

27 **Abstract**

28 *Background*

29 Understanding movement patterns of anadromous fishes is critical to conservation  
30 management of declining wild populations and preservation of habitats. Yet, infrequent  
31 observations of individual animals fundamentally constrain accurate descriptions of movement  
32 dynamics.

33 *Methods*

34 In this study, we synthesized over a decade (2006–2018) of acoustic telemetry tracking  
35 observations of green sturgeon (*Acipenser medirostris*) in the Sacramento River system to  
36 describe major anadromous movement patterns.

37 *Results*

38 We observed that green sturgeon exhibited a unimodal in-migration during the spring months but  
39 had a bimodal distribution of out-migration timing, split between an ‘early’ out-migration (32%)  
40 group during May - June, or alternatively, holding in the river until a ‘late’ out-migration (68%),  
41 November - January. Focusing on these out-migration groups, we found that river discharge, but  
42 not water temperature, may cue the timing of migration, and that fish showed a tendency to  
43 maintain out-migration timing between subsequent spawning migration events.

44 *Conclusions*

45 We recommend that life history descriptions of green sturgeon in this region reflect the distinct  
46 out-migration periods described here. Furthermore, we encourage the continued use of  
47 biotelemetry to describe migration timing and life history variation, not only this population but  
48 other green sturgeon populations and other species.

49

50 **Keywords:** Acoustic telemetry, freshwater, intraspecific variation, migration, rivers, sturgeon

## 51 **Background**

52 Humans modify waterways to suit energy, industrial, agricultural, and drinking water  
53 needs, and these modifications impact the life-histories of migratory fishes. For example, dams  
54 and diversions change river flow patterns and often reduce discharge rates in natural channels,  
55 present direct barriers to fish movements, and cause loss of essential feeding, spawning, and  
56 nursery habitats (1–3). Yet poor understanding of species life-histories often results in  
57 infrastructure that fundamentally blocks migrations or are otherwise not wildlife-friendly (4,5).  
58 As a result, conservation and management efforts often focus on restoring functionality to  
59 riverine systems by removing barriers or through modifications that provide for fish passage  
60 around barriers (6,7). These efforts are attempts to balance human needs (i.e., ecosystem  
61 services) with the ecological requirements of the other organisms that depend on these systems  
62 (7).

63 Life history strategies vary not only among but also within species, with both inter- and  
64 intraspecific diversity contributing to community structure and stability (8,9). Intraspecific  
65 variation may buffer populations from stochastic events that affect certain locations or time  
66 periods, e.g., through portfolio effects (10–12). Chinook salmon (*Oncorhynchus tshawytscha*)  
67 can broadly be described as migrating to oceans as smolts and spending several years growing  
68 and maturing in salt water before returning to their natal streams and rivers (13). However,  
69 Chinook salmon also exhibit variation in migration timing of adults and smolts (14–16). In  
70 comparison to the temporal variability in Chinook salmon migration, striped bass (*Morone*  
71 *saxatilis*) in the Hudson River Estuary migrate different distances to spawning sites and maintain  
72 these site preferences across years (17), effectively dispersing reproductive effort across multiple  
73 sections of the river. Both temporal and spatial intraspecific variation have implications for the

74 populations involved and fisheries that use this natural resource. Effective management of wild  
75 populations requires understanding diversity in migratory tactics, but intraspecific variation may  
76 be hard to document while monitoring wild fishes.

77         Along the Pacific coast of North America, green sturgeon (*Acipenser medirostris*) are a  
78 long-lived, intermittent spawning fish of conservation concern. The southern distinct population  
79 segment (sDPS) in the Sacramento River of California is listed as ‘threatened’ under the US  
80 Endangered Species Act (ESA), and throughout their range, green sturgeon are listed under  
81 CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora)  
82 Appendix II (<https://cites.org>) (18,19). A conceptual model of sDPS green sturgeon movements  
83 described adult green sturgeon migrations as following these general steps: (1) in-migration to  
84 the river occurs during the spring months, peaking in March, with fish travelling over 400 km  
85 upriver to spawning grounds; (2) spawning occurs during the late spring months (April through  
86 June); (3) adults then spend the summer months in the river near to spawning grounds; (4) out-  
87 migration to the Pacific Ocean happens over an extended period in the late summer through  
88 autumn months; (5) individuals then remain in the Pacific Ocean for 2–4 years between  
89 migration events (see 20 for details). Conceptual models like these are valuable for general life  
90 history descriptions of wild animals but can be improved upon when high-resolution data on  
91 movements of individuals become available.

92         The specific objectives of this study were to synthesize the long-term movement profiles  
93 of individual green sturgeon from acoustic telemetry to (1) describe timing of green sturgeon  
94 migrations in the Sacramento River; (2) determine if swim-down events were correlated with  
95 environmental variables (discharge and temperature); and (3) evaluate whether individuals  
96 exhibited fidelity to a particular pattern in migration timing across migration events. We

97 expected upriver migrations in the spring months would occur over a single period so that adult  
98 green sturgeon arrived at spawning grounds when conditions were optimal for the development  
99 of eggs and larvae. We did not have similar expectations for out-migration movements. Past  
100 observations of green sturgeon have described out-migrations occurring across a span of several  
101 months (21,22), including two pulses of downriver movements in the Klamath and Trinity rivers  
102 (northern distinct population segment, see 23).

103

## 104 **Materials & Methods**

### 105 *Study system and acoustic tagging*

106         The lower Sacramento River system of California, defined here as the portion of the river  
107 below the Keswick dam (40.612°, -122.446°), is over 400 km long and is fed by multiple  
108 tributaries before it joins the San Francisco Estuary and the Pacific Ocean. This is among the  
109 planet's most human-altered river systems: flow pathways, discharge rates, and fish habitat are  
110 all subject to human control (24), and the Sacramento River system remains an area of great  
111 conservation interest. The Sacramento River system is perhaps most widely known for its  
112 Chinook salmon (*Oncorhynchus tshawytscha*; e.g., 25) and steelhead trout (*Oncorhynchus*  
113 *mykiss*; e.g., 26), but it is also the central hub for a rich and highly endemic assemblage of fishes  
114 in California (27). It is also a highly threatened fauna, with an estimated 83% of species currently  
115 classified as in some form of decline (28).

116         Over 300 acoustic receivers (VR2W-69 kHz, Innovasea Inc., Halifax NS, Canada; Fig. 1)  
117 have been deployed throughout the Sacramento River, the Inland Delta, the San Francisco  
118 Estuary, and nearshore regions of the Pacific Ocean to passively monitor the movements of  
119 tagged fish (see also 21,22). During the lifetime of these acoustic telemetry projects, deployment

120 configurations and receiver coverage have varied to address the questions of specific projects.  
121 However, there was consistent coverage throughout much of the Sacramento River system  
122 during the 12-year observation period (2006-2018) used in this study.

123 From 2002 to 2014, green sturgeon were surgically implanted with 10-year lifespan  
124 acoustic transmitters (n = 350 tagged sturgeon considered for analysis) by scientists from 13  
125 agencies and research groups (21,22,29,30). Tagging and capture methods varied slightly across  
126 agencies and research groups and over time but were consistent in the following respects. Fish  
127 tagged and released were caught by trammel or gillnets at multiple locations in the Sacramento  
128 River, San Pablo Bay, and Suisun Bay. Nets were either watched for movement in float lines or  
129 soaked for a maximum of 30 min to minimize capture stress on green sturgeon. Fish selected for  
130 tagging were inverted to initiate a tonic immobility-like state and water flow was provided  
131 continuously across their gills. The surgical procedure for these fish is outlined in Miller et al.  
132 (22) but is reviewed briefly here. A small incision, approximately 30 mm, was made anterior to  
133 the pelvic girdle and offset from the midline. Green sturgeon were tagged with V16 (n = 322),  
134 V13 (n = 5), or V9 (n = 23) transmitters, depending on the size of the fish being tagged  
135 (Innovasea Inc., Halifax, NS Canada). Transmitters were inserted into the body cavity and the  
136 incision closed with two to three simple interrupted sutures (PDS II Violet Monofilament,  
137 absorbable) tied with 2x2 surgeon's knots. This general surgical method has been employed  
138 successfully on multiple fishes, including sturgeon, and has been shown to not impact survival,  
139 growth, or swimming performance of juvenile green sturgeon (31). In total, the surgical period  
140 lasted approximately 5 minutes, after which the fish were immediately released at the site of  
141 capture or, if showing signs of stress, temporarily held in an aerated stock tank until they  
142 resumed normal responses.

143

144 *Data selection and longitudinal profiles*

145         The Interagency Telemetry Advisory Group (ITAG) within the Interagency Ecological  
146 Program (IEP), formerly California Fish Tracking Consortium (CFTC), has coordinated the  
147 telemetry efforts of multiple agencies and researchers throughout the Central Valley of  
148 California. As part of the research coordination effort, the BARD database established through  
149 the UC Davis Biotelemetry Lab ([http://cftc.metro.ucdavis.edu/biotelemetry-autonomous-real-](http://cftc.metro.ucdavis.edu/biotelemetry-autonomous-real-time-database/landingmap)  
150 [time-database/landingmap](http://cftc.metro.ucdavis.edu/biotelemetry-autonomous-real-time-database/landingmap)) has been used to compile detections records across a greater scale  
151 than a single organization could compile. The BARD data repository has provided spatial and  
152 temporal resolution to facilitate synthesis-based studies of green sturgeon across multiple  
153 projects and tagging efforts. We accessed green sturgeon detection data from 2006 through 2018  
154 from the BARD database (see above). For individual green sturgeon, we compiled detection data  
155 across the Sacramento River system to create an ordered series of detections that included time  
156 stamps of detection, location of receivers recording each detection, and river km (measured as  
157 distance from the entrance to the Pacific Ocean marked by the Golden Gate Bridge in San  
158 Francisco Bay, hereafter ‘rkm’).

159         Green sturgeon longitudinal detection profiles based on rkm were used to determine  
160 when fish were moving into and out of the river system (see Fig. 1 for general area categories).  
161 When a fish was first detected downriver and then upriver in the same calendar year, the date of  
162 the first record above rkm 105 was logged as the ‘up-date’ and considered when the fish began  
163 migration upriver, presumably to spawn. We selected the 105 rkm value to reflect transition from  
164 Suisun Marsh and the inland Delta region into the Sacramento River proper (Fig. 1). When a fish  
165 was detected upriver in a calendar year and then detected downriver within 500 days of the



166 beginning of that calendar year, the date of first record below rkm 400 was classified as the  
167 ‘down-date’ and recorded as the day outmigration commenced. We selected a value of 400 rkm  
168 as the threshold separating spawning and holding grounds from the rest of the river based on  
169 visual inspection of movement paths (see Supplemental Materials Fig. S1) and previously used  
170 thresholds (32) based on descriptions of green sturgeon activity in the Sacramento River (20).

171 To describe the distribution of days fish either began moving up the Sacramento River or  
172 began their out-migration back down the river, a cumulative distribution function tallying the  
173 observed event dates (see above) was used. If we observed a plateau in dates consistent across  
174 observation years, i.e., a period during which no migration events are observed, the mid-value of  
175 the plateau was used as a dividing value between groups.

176 Because green sturgeon migrations often spanned more than one calendar year, day of the  
177 year alone could not be used to measure migration timing. Rather, we tabulated day counts  
178 relative to the year that a green sturgeon began upriver migration runs, e.g., a fish that migrated  
179 upriver on 1 March, 2017 and downriver on 5 January, 2018 would have been described as  
180 moving upriver on Day 60 and downriver on Day 370. Dates calculated using this method are  
181 referred to as ‘journey dates’ and were all calculated relative to 1 January of the year that a green  
182 sturgeon began an upriver migration.

183 Many green sturgeon were tagged in the Sacramento River during spring months,  
184 presumably already on a spawning run up the river at time-of-tagging, with 71 sturgeon tagged  
185 between rkm 150 and 518. For these fish, the first detected migration event using the criteria  
186 outlined above was their downriver migration. As such, the greater number of downriver  
187 migration events observed (n = 224 events) as compared to upriver migration events (n = 129  
188 events) was attributed primarily to tagging in the river. We established upriver and downriver

189 migration dates representing the complete history of a migration event, referred to as ‘paired up-  
190 down dates’ for 117 migration events during the observation period.

### 191 *Environmental data*

192 We collated environmental data from multiple long-term monitoring stations in the  
193 Sacramento River. We compiled upriver environmental data spanning the study period from two  
194 stations: discharge rates were retrieved from records of the ORD station (California Department  
195 of Water Resources, National Wildlife Refuge Ord Bend Unit; 39.628°, -121.993°) and  
196 temperature data from the RDB station (US Forest Service, Red Bluff Recreation Area; 40.154°,  
197 -122.202°). These stations are located ~60 km apart but chosen for having the most complete  
198 records covering the observation period and their proximity to upriver habitats used by green  
199 sturgeon. For downriver sites, we collected data from two stations: discharge rates from the DTO  
200 station (California Department of Water Resources, Delta out discharge station; 38.059°, -  
201 122.025°) and temperature data from the RVB station (California Department of Water  
202 Resources, Rio Vista Bridge; 38.160°, -121.686°), which were approximately 30 km apart.

### 203 *Environmental variables and migrations*

204 For each up- or down-river migration event that could be determined from acoustic  
205 detections, we created profiles of discharge and temperature for the 21 days surrounding the day  
206 of migration. Each date that a migration was deemed to have commenced (either upriver or  
207 downriver) was designated Day 0; we then extracted river discharge and temperature data from  
208 the 14 d prior to that date and the 7 d afterwards to form a profile around each migration event. A  
209 corresponding segment of environmental data (discharge and temperature) was extracted from  
210 the matched dates using the stations outlined above, i.e., DTO/RVB for upriver and ORD/RDB  
211 for downriver profiles. Once profiles were created for individual fish, the mean values across all

212 fish for discharge and temperature in each of the 22-days was determined to provide a qualitative  
213 description of these parameters in relation to migration events.

214 We had *a priori* interest in downriver migrations due to the extended total duration over  
215 which they have been previously observed to occur. We therefore used semiparametric Cox  
216 proportional hazard regression (hereafter CPH) (33) to determine whether temperature and/or  
217 discharge characteristics were predictive of downriver migrations. Environmental parameters and  
218 swim down events were binned into 5-d intervals. The covariates of mean temperature and  
219 discharge were tested for collinearity (34) during the ‘early’ and ‘late’ out-migration periods  
220 based on variance inflation factor (VIF) scores. Both the ‘early’ and ‘late’ out-migration groups  
221 ( $VIF \leq 1.17$ ) were found to be below the collinearity threshold for collinearity of 5.0 (34,35).  
222 Within each 5-d interval, we determined the mean discharge ( $m^3 s^{-1}$ ), minimum daily discharge  
223 ( $m^3 s^{-1}$ ), and mean water temperature ( $^{\circ}C$ ). We also considered the percent change in mean  
224 discharge ( $\Delta$  discharge) and percent change in mean water temperature ( $\Delta$  temperature)  
225 calculated as the change between subsequent time intervals, i.e.,  $((Temp_{(t+1)} - Temp_{(t)}) / Temp_{(t)})$   
226  $\times 100$  and  $((Discharge_{(t+1)} - Discharge_{(t)}) / Discharge_{(t)}) \times 100$ .

227 The CPH model can be described by the formula

$$228 \quad h(t) = h_0(t) \times \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i),$$

229 where  $h(t)$  is the “expected hazard” at time  $t$ ,  $h_0(t)$  represents the “baseline hazard” assuming no  
230 effect of any covariates, and  $\beta_i$  is the regression coefficient for an explanatory variable ( $X_i$ ). A  
231 hazard ratio (HR) independent of time ( $t$ ) was estimated for each explanatory variable ( $X_i$ ) based  
232 on the regression coefficients determined in the CPH model ( $HR = \exp(\beta_i)$ ). A positive  
233 regression coefficient, and consequently HR value  $> 1$ , for a covariate indicates a positive  
234 relationship between that covariate and, in this case, greater migration probability; larger values

235 of HR indicate a greater probability of migration for each unit increase in the explanatory  
236 variable. The CPH models were fitted using the *coxph* function in the *survival* analysis R  
237 package (36). The proportional hazard for each covariate is assumed, by the CPH approach, to be  
238 independent of time; this was tested using the Schoenfeld residuals (*cox.zph* function), with  $p >$   
239 0.05 for each covariate in the model considered passing this assumption. Due to violations of this  
240 assumption when including migration year as a continuous variable, we included year as a  
241 stratification factor.

242 We used an information-theoretic model selection process that considered models  
243 including all possible combinations of the five covariates outlined above. Using Akaike's  
244 Information Criterion (AIC), the model with the lowest AIC score was identified as the most  
245 supported model ( $\Delta\text{AIC} = 0$ ), but all models with  $\Delta\text{AIC} < 4$  were considered competitive  
246 (Arnold 2010). The relative importance for each covariate was determined by summing the AIC  
247 weights of the models in which they occurred. CPH model coefficients were determined by using  
248 model averaging across the 90% confidence set of models (37,38) using the *dredge* and  
249 *model.avg* functions of *MuMIn* R package (39).

250

### 251 *Repeatability in timing of migration events*

252 Due to the duration of monitoring covered in this study, some fish made more than one  
253 migration up and down the river. Where multiple migration events occurred for the same fish, it  
254 was possible to compare the first and second swim down dates to determine if the timing of  
255 migration was correlated across events. To determine if there was repeatability in the timing of  
256 migrations, journey days were correlated between (i) first and second upriver migrations, (ii) first  
257 and second downriver migrations, and (iii) upriver and downriver migrations. If individuals were

258 observed making more than two migrations during the observation period, only the first and  
259 second event were considered. Normality was tested with the Shapiro-Wilk test. If normality  
260 was violated ( $P < 0.05$ ) for either of the two variables for which correlation was to be computed,  
261 Spearman's rank correlation was used, otherwise Pearson's correlation was used. For correlation  
262 testing purposes, only paired migration events with both up and down dates observed were  
263 considered because up and down movement dates were involved in the comparisons; this  
264 constraint was applied for the up/up and down/down comparisons, as well as for the up/down  
265 comparisons, to produce a consistent dataset on which all the correlation results were based.

266         Given the presence of two distinct out-migration groups (see Results), we evaluated if the  
267 number of fish observed switching between groups from their first to their second trips down the  
268 river was more compatible with consistency or randomness through time of individual fish  
269 departure timing. A randomization trial performed in MatLab (version R2021a, updated 13 April  
270 2021) was used to test the null hypothesis that fish selected their downriver migration group at  
271 random and that the out-migration timing during the second event was not related to the first  
272 event. For each simulation, the same number of fish observed in the field making multiple  
273 migration events ( $n = 64$ ) were randomly assigned to either an 'early' (journey day  $< 250$ ) or  
274 'late' (journey day  $> 250$ ) out-migration group (first migration), and then independently assigned  
275 to a second 'early' or 'late' group (second migration). Probabilities for assignments were based  
276 on empirical values. The number of fish that switched out-migration timing, i.e., 'early-to-late'  
277 or 'late-to-early', was tallied to determine the total number of switches that occurred in the  
278 simulation. This process was repeated for 100,000 simulations to generate a distribution of  
279 numbers of migration timing switches that would be expected if migration timing was random  
280 and independent across events. The empirical number of switches was then compared to the

281 distribution of simulated values, and if the observed number was within the 95% confidence  
282 interval of the simulated values, fish were considered to show significant consistency, through  
283 time, in their migration group choice. All fish were included in this analysis for which at least  
284 two downriver dates were available.

285         To determine if river discharge was related to repeatability in the migration timing of  
286 fish, we first determined if there was a linear relationship between the journey-day departure  
287 timing of first and second out-migration events for fish that departed ‘early’ for both migrations  
288 (i.e., ‘early-early’ fish). Because there was evidence that ‘early-early’ fish out-migration journey  
289 days were strongly correlated between migrations (see Results), the out-migration dates for fish  
290 that switched groups between events (i.e., ‘early-to-late’,  $n = 13$ , and ‘late-to-early’,  $n = 8$ ) were  
291 used to estimate matched dates for the ‘early’ period for the year they migrated ‘late’ based on  
292 the regression relationship determined for ‘early-early’ fish. For each of the fish that switched  
293 migration groups this provided an observed ‘early’ migration date (either first or second  
294 migration) and regression-inferred ‘early’ date (i.e., for the year the individual was observed  
295 migrating ‘late’). Mean flow over a 7-day period leading up to the out-migration dates was  
296 determined for the years fish were observed departing ‘early’ and compared to the years in which  
297 they instead held over and departed as part of the ‘late’ group. Discharge was compared between  
298 the two groups (observed ‘early’ departure and regression-matched ‘early’ dates) using a paired  
299 Wilcoxon rank sums test. Here, we systematically evaluated river flow during actual ‘early’  
300 departures compared to matched ‘early’ times when a fish could, in principle, have departed but  
301 instead chose to migrate ‘late’.

302

## 303 **Results**

304           Based on the tagging records of 350 individual green sturgeon, 151 individuals were  
305 detected in the Sacramento River system during 2006–2018. Nine fish were tagged prior to the  
306 beginning of the observation period (2003–2005), while the remainder of green sturgeon were  
307 tagged 2006–2013 (2006, n = 21; 2008, n = 10; 2009, n = 29; 2010, n = 18; 2011, n = 46; 2012, n  
308 = 16; 2013, n = 2). Average fork length of green sturgeon tagged (mean  $\pm$  1 S.E.) was  $1726 \pm 16$   
309 mm. Fish of both sexes were represented in the sample (females = 15, males = 35), but most  
310 green sturgeon were not sexed (n = 101) during tagging due to logistical and permitting  
311 constraints.

312           A total of 129 upriver migrations and 224 downriver movements were identified (Table  
313 1), including 117 paired detection events (n = 85 unique sturgeon) covering the full migration  
314 sequence (i.e., migration upriver to spawning grounds and subsequent out-migration back  
315 downriver to the Pacific Ocean). When considering all downriver movements including  
316 migration events without a corresponding upriver date, there were 62 green sturgeon that made  
317 more than one downriver migration during the observation period with a mean interval between  
318 downriver migration events of 4.3 years (1562 days).

319

### 320 *Timing and duration of migration*

321           Across all observation years, the 117 paired migration events began with green sturgeon  
322 swimming into the Sacramento River on  $22 \text{ Mar} \pm 22$  days (range 10 Feb – 14 Jun) (see Table 2  
323 for individual year summaries). Across all fish, mean date of outmigration was  $16 \text{ Oct} \pm 93$  days  
324 (min. 15 Apr, max. 24 Mar of year following upriver migration) and individual green sturgeon  
325 were present in the Sacramento River for an average of  $204 \pm 97$  days (Fig. 2a). Upriver

326 migration dates followed a unimodal distribution that peaked in late Mar to early Apr (Fig. 2b).  
327 In comparison, downriver migration dates followed a bimodal distribution (Fig. 2c), with some  
328 green sturgeon returning downriver during May – Jun, and others remaining for several months,  
329 out-migrating to the Pacific Ocean during Nov – Jan (Table 2). All tagged green sturgeon  
330 returned to the Pacific Ocean after a holding period, and there was no evidence of permanent  
331 river-residency by any tagged fish.

332 Based on the distributions of downriver migration dates we defined two swim-down  
333 groups, ‘early’ fish migrated downriver before Sep (< day 250) and ‘late’ fish spent a period of  
334 several extra months in the upper Sacramento River before returning to the Pacific Ocean during  
335 late autumn and early winter (> day 250; Fig. 2). Across the 117 paired up-down migration  
336 events, we observed 37 early return events (n = 34 unique individuals) that spent 76 days in the  
337 river system from swim up to swim down (range 26 – 142 days). In comparison, there were 80  
338 late return events (n = 71 unique individuals) with fish spending a mean of 263 days in the river  
339 (range 139 – 368 days).

340 ‘Early’ returning green sturgeon began their downriver migration on 12 Jun  $\pm$  31 days  
341 (min. 15 Apr, max. 17 Aug) and ‘late’ returning fish began their migration on 14 Dec  $\pm$  37 days  
342 (min. 22 Sep, max. 24 Mar of the year following migration). The days ‘early’ out-migration  
343 began occurred at higher water temperatures and lower discharge levels (mean  $\pm$  1 S.E.,  
344 interquartile range; temperature:  $14.88 \pm 0.22$  °C, IQR = 2.11 °C; discharge:  $227.66 \pm 11.20$  m<sup>3</sup>  
345 s<sup>-1</sup>, IQR = 119.28 m<sup>3</sup> s<sup>-1</sup>) as compared to the ‘late’ out-migration group (temperature:  $11.20 \pm$   
346  $0.18$  °C, IQR = 2.32 °C; discharge:  $346.00 \pm 21.32$  m<sup>3</sup> s<sup>-1</sup>, IQR = 195.12 m<sup>3</sup> s<sup>-1</sup>) (see Fig. S2 and  
347 S3 for further details).



348 *Environmental variables and migrations*

349         Based on the unimodal distribution of upriver migrations and bimodal distribution of  
350 downriver dates described above, we described green sturgeon as migrating ‘upriver’ in a single  
351 group and out-migrating in two distinct groups based on timing (‘early’ and ‘late’). We created  
352 22-day profiles relating discharge and water temperature to each of these three movement  
353 groups. Based on these profiles, green sturgeon began upriver movements during periods of  
354 increasing temperature as winter concluded (Fig. 3a). There was no visually detectable pattern in  
355 discharge and timing of downriver migration in the ‘early’ out-migration group (Fig. 3b), but  
356 there was a tendency for the ‘late’ out-migration group to begin downriver movements after an  
357 initial increase in discharge (Fig. 3c). Downriver migrations did not have apparent correlations to  
358 water temperature.

359         There were ten competitive models for the ‘early’ out-migration period ( $\Delta\text{AIC} \leq 2.78$ )  
360 and 15 for the ‘late’ out-migration period ( $\Delta\text{AIC} \leq 3.90$ ; Table 3). Relative importance among  
361 possible covariates in the ‘early’ group was highest for minimum discharge (0.98), followed by  
362  $\Delta$  discharge (0.73), mean discharge (0.46),  $\Delta$  temperature (0.36), and was lowest for mean  
363 temperature (0.34). In the ‘late’ out-migration group, relative importance was highest for  
364 minimum discharge (0.93), followed by  $\Delta$  discharge (0.55), mean discharge (0.44), mean  
365 temperature (0.43), and  $\Delta$  temperature (0.42).

366         Model averaging of the 90% confidence sets found that in ‘early’ out-migrants, minimum  
367 discharge was significantly related to sturgeon beginning downriver migrations, but the  
368 confidence intervals for all other variables spanned 0 and, therefore, they were considered non-  
369 significant effects (Table 4). Green sturgeon likelihood of departure was positively related to  
370 minimum discharge values within a 5-d time interval (Hazard ratio = 1.48). Among green

371 sturgeon that adopted the ‘early’ out-migration strategy, fish were more likely to depart at higher  
372 minimum discharge values—the mean minimum daily flows for the 5-d intervals when fish  
373 began their downriver migration was  $218 \text{ m}^3 \text{ s}^{-1}$  (range 118 to  $396 \text{ m}^3 \text{ s}^{-1}$ ).

374 Most green sturgeon migration events (68%) were classified into the ‘late’ out-migration  
375 group. Based on CPH model averaging, the timing of out-migrations in this group was related to  
376 the minimum discharge levels (HR = 1.03), but based on confidence intervals was not related to  
377 other variables (Table 4). Changes in discharge during the period of ‘late’ out-migrations  
378 included seasonal influxes of water that increased magnitude and variability in discharge, and  
379 also included a decline in the overall minimum discharge rate, with a 33% decline in minimum  
380 discharge from  $187 \pm 24 \text{ m}^3 \text{ s}^{-1}$  at the beginning of the ‘late’ period to  $126 \pm 25 \text{ m}^3 \text{ s}^{-1}$  over a  
381 period of 150 days. Considering both the 22-day profiles (Fig. 3) and CPH results, green  
382 sturgeon adopting a ‘late’ out-migration timing were likely to depart after initial increases in  
383 seasonal discharge rates, but also when minimum discharge levels were higher.

384 *Repeatability of migration timing*

385           There was a positive correlation between the journey days that individuals began upriver  
386 migrations for their first and second observed migrations (Pearson's correlation,  $t = 2.07$ ,  $df =$   
387  $19$ ,  $P = 0.05$ ; Fig. 4a), but there was not a corresponding correlation between journey days that  
388 downriver migrations began (Spearman's correlation,  $\rho = 0.29$ ,  $P = 0.20$ ; Fig. 4b). There was  
389 no correlation for the journey days that fish began migrating upriver and the day they began to  
390 move back downriver, i.e., individuals that migrated upriver earlier in the spring run did not  
391 necessarily return to the Pacific Ocean earlier (Spearman's correlation,  $\rho = -0.09$ ,  $P = 0.56$ ;  
392 Fig. 4c).

393           Comparing swim down classifications between the first and second swim down events,  
394 10 sturgeon adopted an 'early-early' strategy as compared to 13 with an 'early-late' strategy,  
395 representing 56% of fish changing from 'early' to 'late' timing between their first and second  
396 migrations (Fig. 5). In comparison, 33 fish adopted a 'late-late' strategy, with 8 fish (20%)  
397 changing strategy between migration periods (i.e., a 'late-early' strategy). Across all years of the  
398 observation period, we documented a total of 21 fish switching out-migration groups between  
399 their first and second migration intervals (13 fish early to late and 8 fish late to early) compared  
400 to a mean of 28 switches expected under random assignments over 100,000 simulations. The  
401 proportion of fish that switched strategy in these randomizations was found to be marginally  
402 significantly greater than the number observed empirically ( $P = 0.05$ ). We interpreted this as a  
403 tendency for conservation of out-migration timing group between subsequent migrations, and  
404 further investigated the conditions under which a fish might switch strategy.

405           Among the 'early-early' green sturgeon, there was a strong linear relationship between  
406 first and second departure journey days (Second migration day =  $1.685 \times$  First migration day –

407 116.47;  $R^2 = 0.92$ ), but on average fish departed 4 days earlier on their second observed  
408 migration. This estimated relationship was used to get matched dates for switching fish (i.e.,  
409 ‘early-to-late’ and ‘late-to-early’, see Methods for details) and comparisons of mean flow during  
410 the ‘early’ departure period in years fish departed ‘early’ vs. holding to the ‘late’ departure  
411 period. Among the fish that switched migration timing ( $n = 21$ ), river discharge was greater for  
412 the migration event when fish departed in the ‘early’ group (mean  $\pm$  1 S.E.:  $283 \pm 24 \text{ m}^3 \text{ s}^{-1}$ ,  
413 median:  $250 \text{ m}^3 \text{ s}^{-1}$ ) as compared to the discharge levels matched to the ‘early’ period on years  
414 when fish departed ‘late’ (mean  $\pm$  1 S.E.:  $187 \pm 10 \text{ m}^3 \text{ s}^{-1}$ , median:  $189 \text{ m}^3 \text{ s}^{-1}$ ; Wilcoxon rank  
415 sums,  $Z = 205$ ,  $P = 0.001$ ). Therefore, among fish observed switching migration strategy ( $n =$   
416 23), sturgeon were more likely to depart during the ‘early’ period when the Sacramento River  
417 discharge rates were higher.

418

## 419 **Discussion**

420 Biodiversity is currently declining across terrestrial and aquatic environments, but the  
421 rate of diversity loss among freshwater organisms is outpacing that of other major systems (40).  
422 For many species, conservation efforts have been fundamentally constrained by large gaps in the  
423 understanding of complete life-cycles and how species interact with habitats impacted by  
424 humans. Anadromous fishes that periodically enter freshwater rivers for spawning are  
425 emblematic of such challenges because (1) they spend much of their lifetime in ocean  
426 environments where they are rarely observed, (2) they migrate through a diverse array of  
427 habitats upon entering freshwater rivers, and (3) iteroparous species are infrequently observed  
428 across the multiple migration journeys they may make in a single lifetime. Green sturgeon in  
429 California are a prime example of how conservation management of endangered or threatened

430 species must proceed even when we lack detailed information on the life-history and behavioral  
431 ecology of the species. In this study, we provide an example of how long-term biotelemetry  
432 studies can be collated to reveal complexity in behavioral life-histories and describe ecological  
433 characteristics of species directly relevant to conservation actions. Understanding the diversity  
434 and function of intraspecific life-history variability has implications for the management of  
435 species and ecosystems.

#### 436 *Timing of migration events*

437         The unimodal upriver migration of green sturgeon into the Sacramento River during the  
438 spring months, peaking during the month of March, resembled observations of the nDPS green  
439 sturgeon in Oregon (23). The discrete period of spring migrations for green sturgeon was  
440 consistent with selection pressures related to offspring development and survival (e.g., Wright  
441 and Trippel 2009, Tillotson and Quinn 2018). Reproductive success of fish migrating long  
442 distances from their home ranges to spawning grounds (such as sDPS green sturgeon migrating  
443 to California from areas near Vancouver Island; 43) may be under selection to ensure that arrival  
444 coincides with that of potential mates and optimal conditions for offspring development (44).

445         All the tagged green sturgeon returned to the Pacific Ocean with none of the tagged fish  
446 exhibiting permanent residency in the Sacramento River system. Miller et al. (22) reported that  
447 green sturgeon were detected in the Sacramento River system during all months of the year,  
448 raising the potential that the sDPS green sturgeon population includes partial migration  
449 strategies, i.e., some individuals exhibit permanent river residency. River-residents have been  
450 described for other sturgeon species, including lake sturgeon (45–47) and shortnose sturgeon  
451 (*Acipenser brevirostrum*; 48). Furthermore, alternate migration strategies are a common aspect  
452 of salmonid biology in California, presumably as a bet-hedging adaptation for the notoriously

453 variable Mediterranean climate (49–51). Even though some of the green sturgeon monitored in  
454 this study spent over a year in the Sacramento River, they all eventually returned to the Pacific  
455 Ocean and on average returned to the river on a 4-year cycle (Supplemental Materials Fig. S1).  
456 The extended post-spawning holding time for some fish, i.e., the ‘late’ downriver group  
457 identified here, contributed to overlap among upriver and downriver migration groups across  
458 years, which explains the observation of green sturgeon present in the Sacramento River during  
459 all months (22). Given that some fish were present in the Sacramento River for over one year,  
460 there were likely foraging and habitat requirements specific to this residence period which are  
461 worthy of further investigation.

462

#### 463 *Environmental cues of downriver migration*

464 Heublein et al. (21) reported conflicting annual patterns relating discharge to downriver  
465 migrations across study years; these results may be due in part to the use of daily mean discharge  
466 and limited total sample size during initial tracking efforts. Indeed, mean discharge was  
467 considered during CPH model selection, but ranked low in relative importance scoring of  
468 variables ( $\leq 0.46$  in both ‘early’ and ‘late’ groups). River flow characteristics have previously  
469 been described as likely drivers of green sturgeon migration (21). Our analysis across multiple  
470 years and repeated spawning events provided further support for river discharge as a primary  
471 factor influencing out-migration behaviors, particularly minimum discharge rates as measured  
472 across multiple days.

473 In addition to identification of the role minimum discharge for both ‘early’ and ‘late’  
474 migrants in this study, seasonal patterns of flow variation in the system add context inferences of  
475 sturgeon migrations. ‘Early’ out-migrants were largely exiting during early summer months

476 (June) and based on discharge profiles of the Sacramento River (Supplemental Materials Fig.  
477 S2), departed prior to annual lows in river discharge. While there has been interest in fish  
478 stranding occurring due to modifications of waterways, e.g., hydroelectric-related alterations to  
479 water discharge rates, there are natural sources of discharge variation that can also pose risks to  
480 fishes (reviewed by 52). It is possible that evolutionary responses to these natural cycles in river  
481 discharge resulted in cues observed here for the ‘early’ fish to depart the system at a perceived  
482 threshold or wait until levels increased during the winter months (‘late’ group).

483         In contrast to discharge patterns in the early summer months, the ‘late’ downriver group  
484 initiated migration during a period of seasonal discharge increases, and based on the 22-day  
485 profiles began out-migration after an influx of water. The pattern of an initial influx triggering  
486 downriver migration has also been reported for the nDPS green sturgeon (23) and was predicted  
487 for sDPS green sturgeon (53). Fish have been tracked moving downriver in response to changing  
488 discharge levels associated with stochastic events, including striped bass observed egressing the  
489 Hudson River before large-scale storm systems resulted in flow surges (54). Recent studies on  
490 high discharge rates and green sturgeon in the Sacramento River system have focused on factors  
491 impacting fish migrating upriver (55), but seasonal fluctuations in discharge may also influence  
492 evolution of differential out-migration patterns within this population.

493         Green sturgeon migration patterns have been predicted to be related to water temperature  
494 (23). In this study, we found links between discharge rates but not temperature for either out-  
495 migration group identified. Temperature is likely to have impacts on many aspects of green  
496 sturgeon life history, but it does not appear to be a primary factor in the migration patterns for  
497 sDPS green sturgeon (see Supplemental materials for additional discussion about temperature).  
498 Temperature may have a greater impact in rivers further north, e.g., nDPS population of green

499 sturgeon in Oregon and Washington states, but the sDPS green sturgeon did not show patterns of  
500 water temperature predicting out-migration timing.

501

### 502 *Repeatability of migration timing across bouts*

503 Multiple downriver migration groups with timing similar to those in this study have been  
504 reported for nDPS green sturgeon in the Klamath and Trinity rivers (23). In the Sacramento  
505 River system, the ‘late’ downriver group represented most observed migration events (68%), but  
506 the ‘early’ downriver departures still represented a significant portion of the downriver  
507 movements (32%). ‘Late’ departing fish were more likely to depart a second time in the same  
508 out-migration timing group than the ‘early’ departing fish (80% repeatability compared to 44%),  
509 nonetheless still nearly half of the ‘early’ group departed a second time in the ‘early’ group.

510 It has been speculated that rapid spring out-migration could be the result of tagging and  
511 handling effects due to previous observations of white sturgeon abandoning spawning runs  
512 following tagging (56). However, a previous study reported that 71% of green sturgeon tagged  
513 following stranding events in the Sacramento River continued moving upriver after tagging and  
514 release (55). In this study, we observed 62 repeat migration events separated by an average of 4  
515 years and still observed the two distinct out-migration periods; therefore, we suggest ‘early’ and  
516 ‘late’ groups described here are unlikely to be related to tagging or handling effects on green  
517 sturgeon.

518 Repeatability of downriver migration times across spawning bouts was consistent with  
519 differential migration in sDPS green sturgeon. Many individuals did switch strategies, but  
520 overall, we observed a tendency of maintaining out-migration timing between subsequent events,  
521 and we argue that these tactics could be in part condition-dependent life history tactics rather



522 than fixed for a lifetime. Life history variation is particularly of interest in fishes because it is  
523 widespread across taxa and falls into both fixed and conditional strategies (57). For example,  
524 Coho salmon (*Oncorhynchus kisutch*) males exhibit both morphologically distinct jack vs.  
525 hooknose life histories, fixed strategies maintained for the entire lifetime, and fight vs. sneak  
526 behaviors, conditional strategies that can change across reproductive events (58). Here, the  
527 presence of distinct downriver migration groups in green sturgeon may represent aspects of  
528 reproduction-related life history variation but given the ability of fish to switch groups across  
529 spawning bouts, this variation is likely a form of conditional life history strategy that can vary  
530 between reproductive bouts. Indeed, among the 23 fish observed switching between ‘early’ and  
531 ‘late’ strategies, we observed patterns in river discharge that support further consideration of  
532 river flow as the likely mechanism behind conditional switching of out-migration strategies. Our  
533 results comparing flow at early departures with flows at time-matched ‘early’ dates in years  
534 when fish out-migrated late, suggested the possibility that fish have a preferred ‘early’ departure  
535 times which they abandon in favor of a ‘late’ departure when flows are too low during their  
536 preferred ‘early’ time. Though we emphasize data only support this as a hypothesis and further  
537 work is needed, the possibility has intriguing implications for conservation and river flow  
538 management if months-delayed departures cause additional consequences ranging from energetic  
539 costs, particularly for post-spawn females, to risk of mortality.

540

#### 541 *Anthropogenic impacts on life history variation*

542 Anthropogenic impacts on communities may not impact all stages or forms of life history  
543 equally. For green sturgeon, the Red Bluffs Diversion Dam (RBDD) had a long period of  
544 potential impacts on sDPS migration from the mid-20<sup>th</sup> century until its full deactivation in 2013

545 (53,59). For much of its operational history, water gates of RBDD would have been closed  
546 during early summer months when the ‘early’ group would be migrating downriver. If these  
547 gates increased risk—either through injuries or mortality—to this specific group of fish it could  
548 account for some of the disparity observed between the overall number of fish adopting ‘early’  
549 and ‘late’ migrations, especially for a long-lived intermittently spawning species such as green  
550 sturgeon.

551 Increased flows have been associated with increased spawning efficiency of diverse  
552 native fishes in California (60,61), and much focus has been placed on the management of flow  
553 rates to increase spawning success and larval sturgeon survival (reviewed by 20). However, in  
554 this study we also found evidence that adult migration timing may be related to flow  
555 characteristics of the Sacramento River and that when fish experienced lower discharge rates  
556 during the late spring months (‘early’ group here) they may be more likely to hold over for  
557 several months in the river. Prior to its closure, the RBDD controlled water flow to  $283 - 425 \text{ m}^3$   
558  $\text{s}^{-1}$  (May - Sep) (62), which were consistent with the flow rates observed to be correlated with  
559 ‘early’ downriver migration here, but the dam itself presented a barrier to fish movements.  
560 Among the fish that switched between ‘early’ and ‘late’ out-migration timing, we observed lower  
561 flow rates in the years fish switched to a ‘late’ strategy (mean =  $187 \text{ m}^3 \text{ s}^{-1}$ ), suggesting that  
562 facilitating adult green sturgeon migrations during the spring and early summer months will  
563 require more than deactivation of RBDD. Furthermore, if persistent drought conditions continue  
564 to impact river discharge, it is plausible that increasing numbers of green sturgeon will adopt a  
565 ‘late’ out-migration strategy. This extended river-holding behavior raises further questions about  
566 holding locations in the river, resource needs during the extended river holding period,

567 physiological impacts of extended periods in freshwater, and if holding in the river increases  
568 exposure to other threats, e.g., susceptibility to poaching and overall capture risk.

569

## 570 **Conclusions**

571 Our synthesis drew on telemetry data gathered for over a decade and provided further  
572 details on migration timing, identified potential environmental cues to downriver migration, and  
573 described within-population life history variability for the threatened population of green  
574 sturgeon in the Sacramento River. Long-term biotelemetry data therefore holds great potential  
575 for understanding the life-histories of species like sturgeon that conduct large-scale migrations  
576 (63,64). Intraspecific variation in life histories can take many forms within wild populations, but  
577 ecological diversity and behavioral plasticity within populations may also provide buffering  
578 capacity to stochastic events. Individual-based tracking techniques, including acoustic telemetry,  
579 are providing avenues to describe and explore mechanisms of life history variation. These data  
580 are in turn valuable to conservation science aimed at protecting rare and declining species, like  
581 sturgeon. We concluded that the two downriver out-migration groups were robust across time  
582 and represented differential migration patterns based on the timing of movements, and we  
583 encourage their inclusion in conservation planning for sDPS green sturgeon. Furthermore, given  
584 the duration of activity in the Sacramento River and the potential for continued drought-related  
585 conditions causing stress on this populations, we recommend further examination of movement  
586 and habitat use within the upper reaches of the Sacramento River because adult green sturgeon  
587 may face stressors and risks in the river environment that could impact individual fitness and  
588 survival beyond the spawning season alone.

589

## 590 **List of Abbreviations**

591 AIC – Akaike’s information criterion

592 CITES – Convention on International Trade in Endangered Species of Wild Fauna and Flora

593 CPH – Cox proportion hazard regression model

594 ESA – Endangered Species Act

595 HR – hazard ratio (part of CPH above)

596 nDPS – northern distinct population segment of green sturgeon

597 RBDD – Red Bluffs Diversion Dam

598 sDPS – southern distinct population segment of green sturgeon

599 VIF – variance inflation factor

600

## 601 **Declarations**

### 602 *Availability of data and materials*

603 All data regarding green sturgeon movements used in this study was compiled from the

604 University of California Davis biotelemetry database (BARD -

605 <http://cftc.metro.ucdavis.edu/biotelemetry-autonomous-real-time-database/fishtrack>).

### 606 *Competing interests*

607 The authors declare that they have no competing interests.

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614 *Authors' contributions*

615 SFC and LWS compiled all detection data and performed primary analysis and writing on  
616 the manuscript. DRO, DCR, JAW, and ALR provided feedback on all steps of analysis and  
617 manuscript drafts. GPS, JTK, and MT provided contextual support regarding green sturgeon in  
618 the Sacramento River system and comments on various drafts of this work. All authors have read  
619 and approved the final manuscript.

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791 electronic tagging to provide insights into salmon migration and survival. *Environ Biol*  
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793

794 **Table 1.** Counts of the numbers of unique green sturgeon observed undertaking upriver and  
795 downriver migrations in each calendar year (2006 – 2018). See methods for criteria used to  
796 identify that individual green sturgeon were migrating through the Sacramento River system in  
797 each year.

798

<b>Year</b>	<b>Count of upriver migrating fish</b>	<b>Count of downriver migrating fish</b>
2006	2	18
2007	4	3
2008	2	8
2009	3	20
2010	4	34
2011	3	13
2012	18	36
2013	14	5
2014	14	24
2015	20	19
2016	28	28
2017	17	10
2018	0	6
<b>Total</b>	<b>129</b>	<b>224</b>

799 **Table 2.** Count and dates of migrations for green sturgeon divided into in-migration, ‘early’ out-migration, and ‘late’ out-migration  
 800 groups. The mean and range (in parentheses) of dates are presented based on the year a fish was detected migrating up the Sacramento  
 801 River.

802

Year	In-migration		‘Early’ Out-migration		‘Late’ Out-migration	
	Count	Date	Count	Date	Count	Date
2007	4	Apr 9 (Mar 21 – May 17)	1	Aug 17	3	Dec 18 (Dec 7 – Jan 6)
2008	0	--	0	--	0	--
2009	3	Apr 1 (Mar 12 – Apr 23)	0	--	3	Nov 16 (Oct 14 – Jan 14)
2010	3	Mar 21 (Mar 2 – Apr 25)	0	--	3	Dec 9 (Dec 7 – Dec 11)
2011	2	Mar 1 (Feb 23 – Mar 8)	1	Jun 28	1	Jan 23
2012	17	Apr 3 (Mar 6 – May 5)	10	Jun 14 (May 24 – Jul 24)	7	Nov 25 (Nov 21 – Dec 2)
2013	13	Mar 30 (Feb 18 – May 6)	3	Jul 7 (July 1 – Jul 12)	10	Feb 5 (Dec 15 – Feb 14)
2014	13	Mar 21 (Feb 15 – May 5)	3	Jun 11 (May 11 – Jul 26)	10	Dec 4 (Dec 1 – Dec 6)
2015	20	Apr 5 (Feb 18 – Jun 14)	4	Jun 23 (May 20 – Jul 26)	16	Dec 13 (Oct 15 – Jan 9)
2016	26	Mar 20 (Feb 10 – Apr 14)	9	May 21 (April 15 – Jul 7)	17	Nov 13 (Sep 22 – Dec 12)
2017	16	Mar 20 (Feb 24 – May 4)	6	Jun 9 (May 18 – Jul 7)	10	Jan 14 (Nov 22 – Mar 24)

803

804 **Table 3.** Model fit summary for combinations of five covariations related to water discharge and  
 805 temperature predicted to be related to the migration timing of (a) ‘early’ and (b) ‘late’ out-  
 806 migration green sturgeon from the Sacramento River system. Predictor variables for each model  
 807 are shown along with the number of parameters in each model ( $K$ ), log likelihood ( $LL$ ), Akaike’s  
 808 Information Criterion ( $AIC$ ), difference in  $AIC$  score compared to the top model ( $\Delta AIC$ ), and  
 809 model weight ( $w_i$ ). Models up to the first with a  $\Delta AIC$  score  $> 4$  are shown.

810

Model variables	$K$	$LL$	$AICc$	$\Delta AIC$	$w_i$
<b>(a) ‘Early’ out-migration</b>					
$\Delta$ discharge + min discharge	2	-29.52	63.06	0	0.19
$\Delta$ discharge + min discharge + $\Delta$ temp	3	-28.93	63.92	0.86	0.12
$\Delta$ discharge + min discharge + temp	3	-29.00	64.07	1.01	0.11
discharge + $\Delta$ discharge + min discharge	3	-29.14	64.35	1.28	0.10
discharge + min discharge	2	-30.39	64.80	1.74	0.08
discharge + $\Delta$ discharge + min discharge + $\Delta$ temp	4	-28.62	65.34	2.28	0.06
discharge + $\Delta$ discharge + min discharge + temp	4	-28.65	65.40	2.34	0.06
discharge + min discharge + $\Delta$ temp	3	-29.70	65.46	2.40	0.06
discharge + min discharge + temp	3	-29.82	65.69	2.63	0.05
$\Delta$ discharge + min discharge + temp + $\Delta$ temp	4	-28.87	65.84	2.78	0.05
discharge + min discharge + temp + $\Delta$ temp	4	-29.54	67.17	4.10	0.02
<b>(b) ‘Late’ out-migration</b>					
$\Delta$ discharge + min discharge	2	-105.51	215.04	0	0.13
$\Delta$ discharge + min discharge + temp	3	-104.80	215.62	0.58	0.10
$\Delta$ discharge + min discharge + $\Delta$ temp	3	-104.88	215.78	0.74	0.09



discharge + min discharge	2	-106.02	216.05	1.01	0.08
discharge + min discharge + temp	3	-105.12	216.26	1.22	0.07
min discharge + $\Delta$ temp	2	-106.16	216.33	1.29	0.07
min discharge + temp	2	-106.16	216.33	1.29	0.07
discharge + min discharge + $\Delta$ temp	3	-105.16	216.33	1.30	0.07
discharge + $\Delta$ discharge + min discharge	3	-105.51	217.04	2.00	0.05
$\Delta$ discharge + min discharge + temp + $\Delta$ temp	4	-104.51	217.06	2.02	0.05
discharge + $\Delta$ discharge + min discharge + temp	4	-104.80	217.63	2.59	0.04
discharge + $\Delta$ discharge + min discharge + $\Delta$ temp	4	-104.88	217.79	2.75	0.03
discharge + min discharge + temp + $\Delta$ temp	4	-105.10	218.23	3.19	0.03
min discharge + temp + $\Delta$ temp	3	-106.16	218.33	3.29	0.03
discharge + $\Delta$ discharge + min discharge + temp + $\Delta$ temp	5	-104.45	218.94	3.90	0.02
min discharge	1	-108.64	219.29	4.25	0.02

---

811 **Table 4.** Model-averaged Cox proportional hazard parameter estimates for green sturgeon classified into either ‘early’ or ‘late’ out-  
 812 migration groups in the Sacramento River.

813

Covariate	Coefficient ( $\beta$ ) & Confidence Interval	S.E. $\beta$	Hazard Ratio (HR: $e^\beta$ )	HR Confidence Interval
<b>(a) ‘Early’ out-migration</b>				
Min discharge	0.39 (0.14 – 0.65)	0.13	1.48	1.15 – 1.92
$\Delta$ discharge	-0.74 (-2.36 – 0.44)	0.75	0.48	0.11 – 1.55
$\Delta$ temp	-0.10 (-1.75 – 1.06)	0.42	0.90	0.40 – 1.55
Mean temp	-0.24 (-10.85 – 9.11)	2.70	0.79	0.58 – 1.56
Mean discharge	0.02 (-1.09 – 1.19)	0.39	1.02	0.48 – 2.18
<b>(b) ‘Late’ out-migration</b>				
Min discharge	0.04 (0.01 – 0.07)	0.02	1.03	1.00 – 1.07
$\Delta$ discharge	-0.02 (-0.06 – 0.03)	0.02	0.98	0.94 – 1.03
$\Delta$ temp	-0.001 (-0.85 – 0.85)	0.43	0.99	0.43 – 2.33
Mean temp	0.96 (-6.55 – 8.46)	3.83	2.61	0.001 – 4.72
Mean discharge	-0.006 (-0.04 – 0.02)	0.01	0.99	0.96 – 1.02

814 **Figure Captions**

815 **Figure 1.** Positions of receivers throughout the San Francisco Bay, Sacramento River, and San  
816 Joaquin River systems during the 2006 through 2018 observation period used in this study.

817

818 **Figure 2.** Cumulative number of fish migration events (max = 117) commenced by a given day  
819 of calendar year (journey day). Upriver migration (red) were used to determine the calendar year  
820 migrations began and this start year was applied to downriver migrations (blue), therefore,  
821 journey days > 365 indicate a fish that migrated upriver in one calendar year, e.g., 2013, and  
822 migrated downriver the following calendar year, e.g., 2014. The distribution of (b) swim up and  
823 (c) swim down dates are shown relative to a normal distribution.

824

825 **Figure 3.** Profiles of Sacramento River discharge rate ( $\text{m}^3 \text{s}^{-1}$ ) and temperature ( $^{\circ}\text{C}$ ) over a 21-  
826 day period surrounding the day of migration (14 days before and 7 days following migration).  
827 Profiles were created for (a) upriver migration dates, (b) ‘early’ downriver migrations, and (c)  
828 ‘late’ downriver migrations. Day 0 (dashed line) represents the date identified as the beginning  
829 of out-migration. The black line in each panel represents the mean discharge rate or temperature  
830 across all fish for each day and each colored line tracks an individual fish over 22 days.

831 Environmental measures were collected from two stations each for the upriver and downriver  
832 migrations.

833

834 **Figure 4.** Comparison of migration timings (journey days) for individual green sturgeon that  
835 were tracked making more than one complete migration during the study observation period.

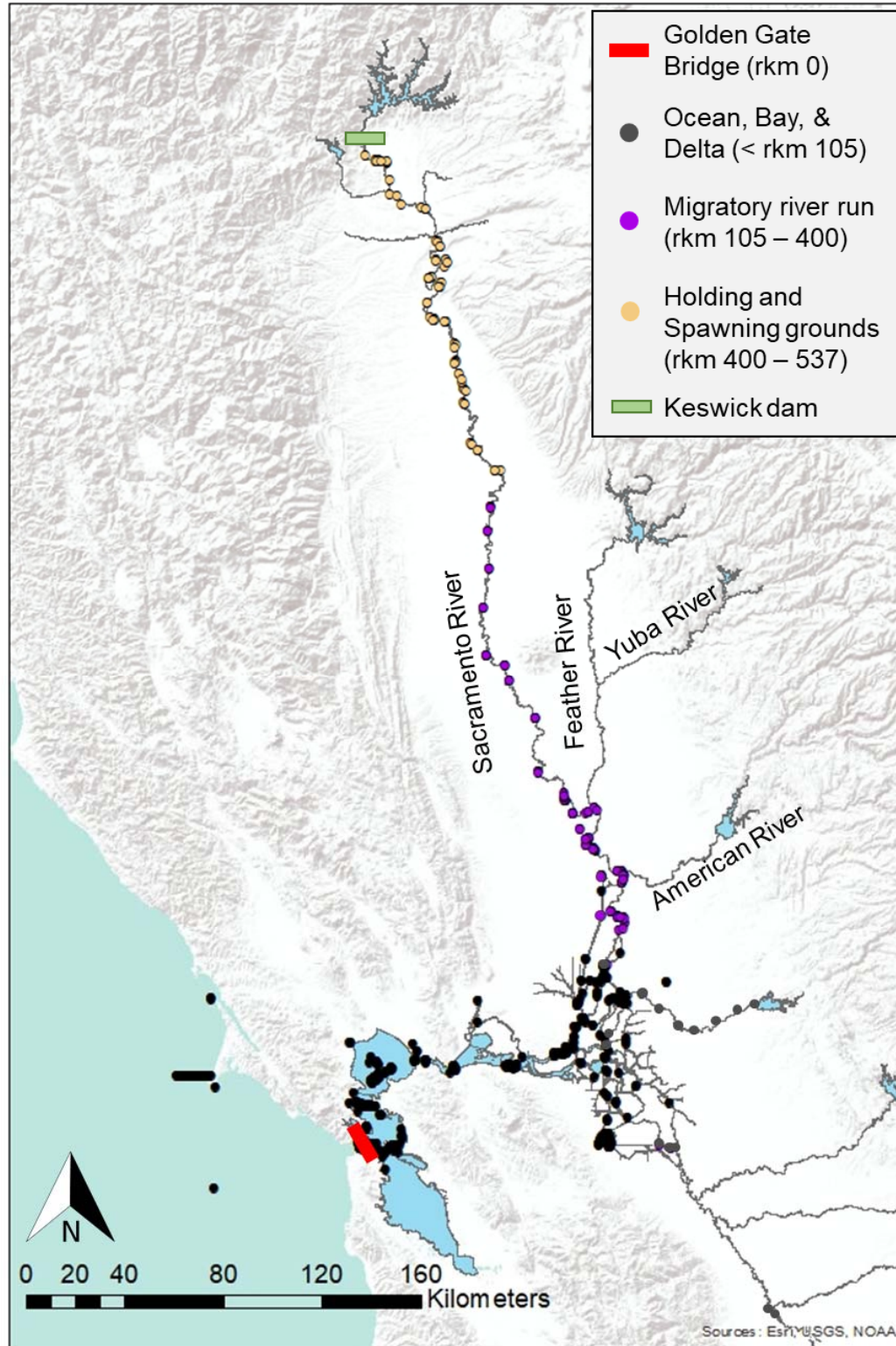
836 Correlations of (a) upriver migration days, (b) downriver migration days, and (c) upriver day and

837 the corresponding downriver date for a given migration are shown. Line of best fit is shown for  
838 correlations determined to be statistically significant. Only individuals with complete detection  
839 records for a given year from the time of entry to the Sacramento River were considered, i.e.,  
840 fish tagged mid-migration in the river system were not included in these correlations because  
841 upriver journey days could not be determined.

842

843 **Figure 5.** Timing of swim down for fish observed making two downriver migrations during the  
844 2006-2018 observation period. Dashed lines represent the journey day 250 cut-off used to  
845 classify early and late swim down groups. For fish tagged mid-migration in the Sacramento  
846 River system the swim down journey date is given assuming they began to migrate upriver  
847 during the calendar year of capture.

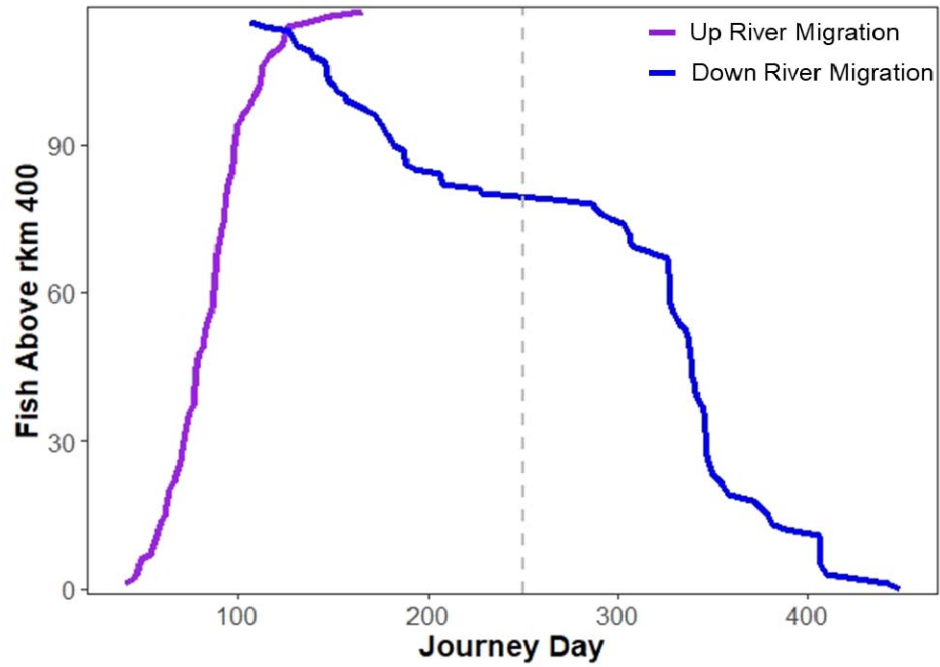
848



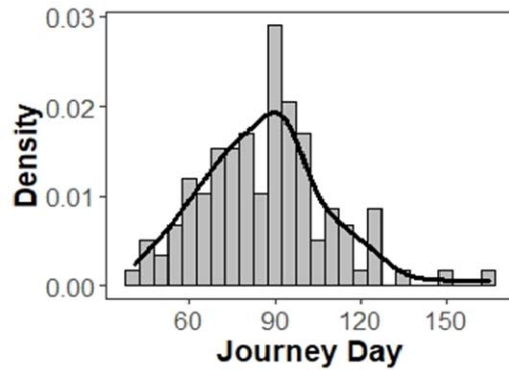
849

850 **Figure 1.**

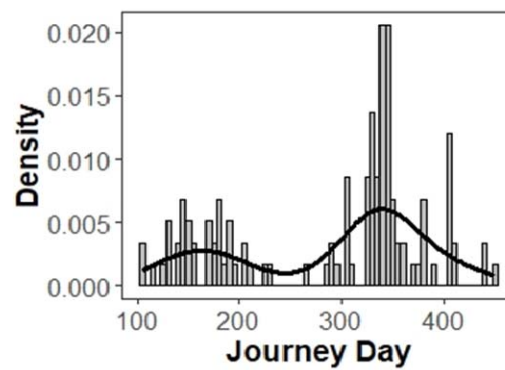
**(a) Number of Sturgeon Up River**



**(b) Distribution of Swim Up Days**

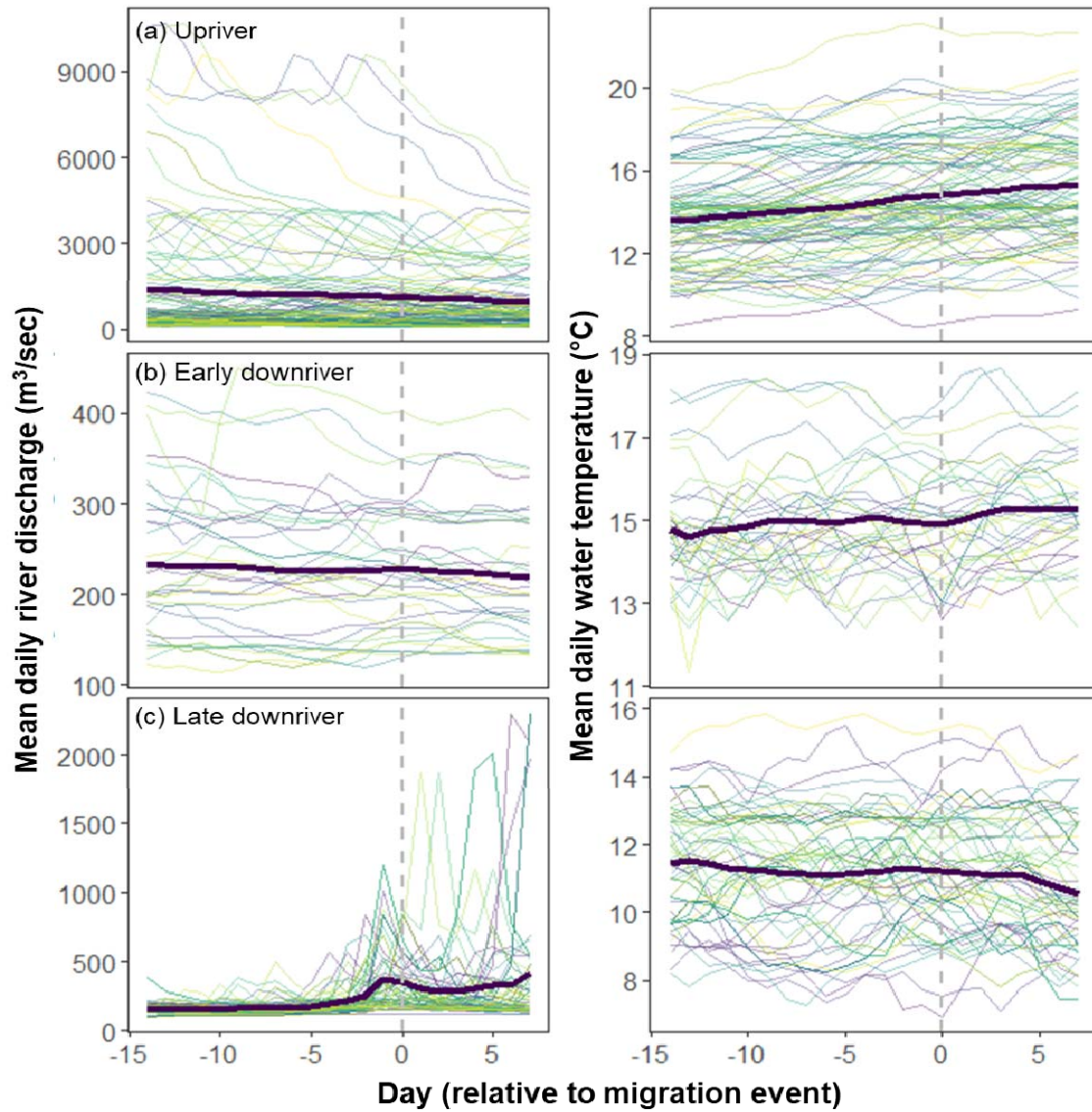


**(c) Distribution of Swim Down Days**



851

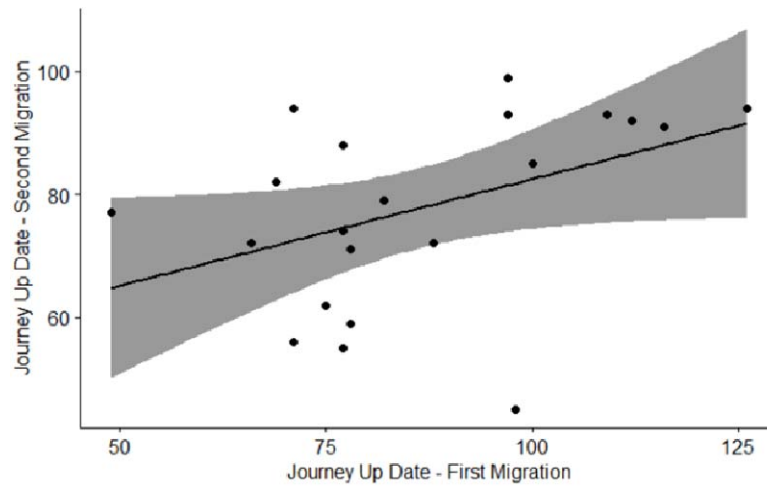
852 **Figure 2.**



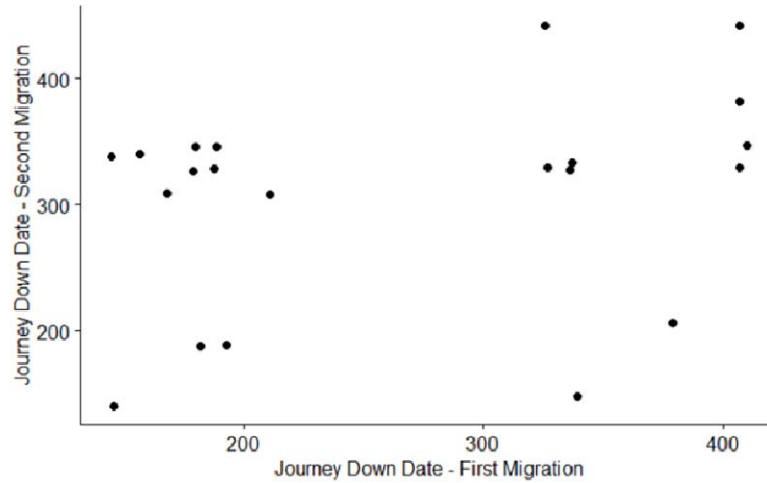
853

854 **Figure 3.**

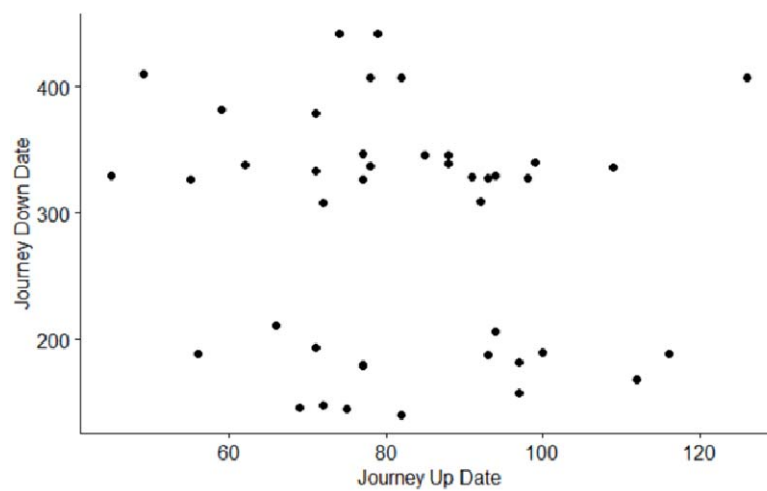
**(a) Upriver migrations**



**(b) Downriver migrations**



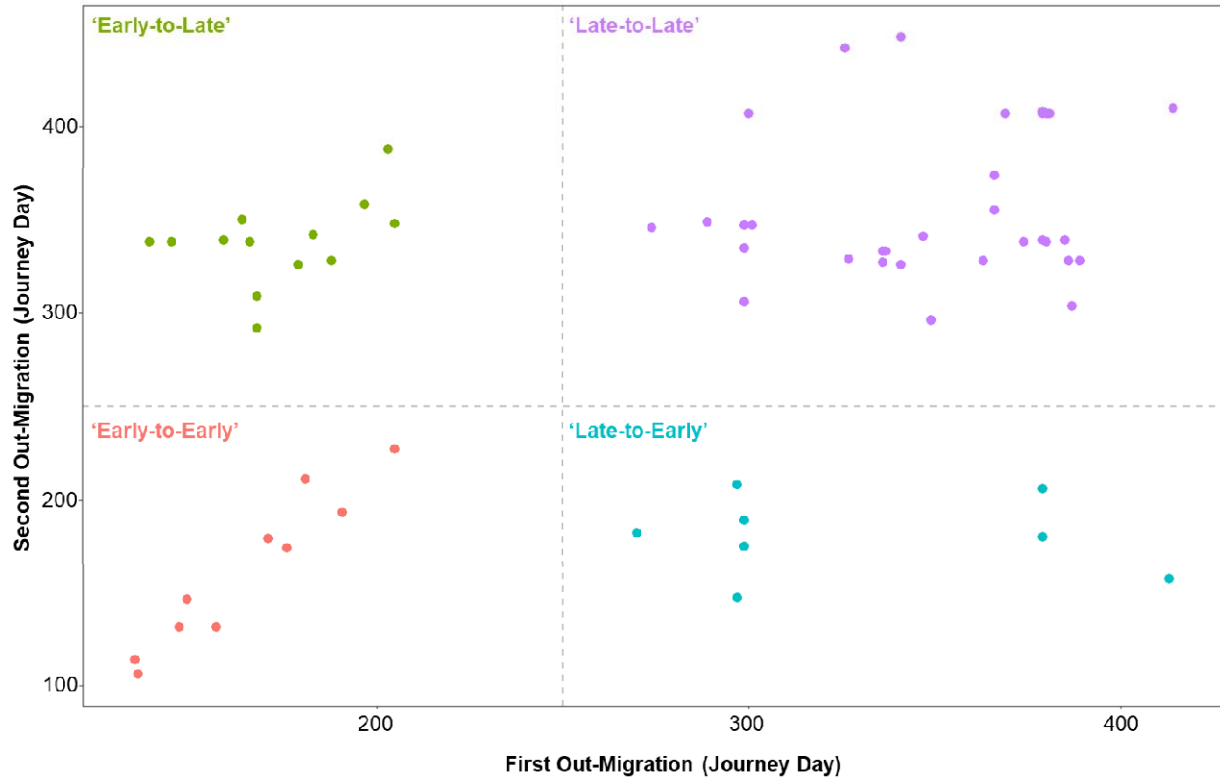
**(c) Upriver – Downriver migrations**



855

856 **Figure 4.**





857

858 **Figure 5.**