1   Age-specific estimates indicate potential deleterious capture effects and low survival of stocked

2   juvenile Colorado Pikeminnow (*Ptychocheilus lucius*)

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22   Running head: Survival of Colorado Pikeminnow

23   Abstract

24   Hatcheries and stocking programs have become necessary to repatriate or augment

25   populations of imperiled fishes worldwide. Over nearly two decades, millions of endangered

26   juvenile Colorado Pikeminnow Ptychocheilus lucius have been stocked into the San Juan River

27   (Colorado, New Mexico, and Utah); however, recruitment of these individuals to adult life stages

28   (age $\geq$6) remains low. Using a mark–recapture data set collected from annual riverwide

29   electrofishing efforts between 2003 and 2016, we investigated apparent survival and capture

30   probabilities of stocked Colorado Pikeminnow to identify age-specific bottlenecks contributing

31   to this lack of recruitment. With relatively high capture rates, which averaged between 0.34 and

32   0.39 for the first 2 years after an individual's first encounter, our results indicated that survival

33   was consistently less than 0.25 for young age-groups (i.e., ages 1–3), and no appreciable increase

34   in survival occurred until fish had been in the river for at least 3 years (i.e., age $\geq$4+). Although

35   age and capture effects were confounded for most age-groups, capture appeared to reduce

36   apparent survival for age-2 fish by approximately 50%. The confounding effects of age, a

37   completely hatchery-origin population, and extensive environmental alterations to the San Juan

38   River make it difficult to disentangle factors associated with this overall reduced juvenile

39   survival.

Introduction

Native fishes worldwide are declining in response to anthropogenic alterations to their environments (Dudgeon et al. 2006; Jelks et al. 2008; Fullerton et al. 2010). To counter these declines, stocking programs developed to repatriate or augment declining populations have become increasingly common to avoid extinction (Seddon et al. 2007; Cochran-Biederman et al. 2015). Ideally, identifying and ameliorating the factors responsible for the initial declines will be requisite for species recovery; however, the immediate conservation concern for many species has forced the implementation of stocking activities to prevent further population declines (Shute et al. 2005). Although these programs can temporarily alleviate the threat of local extirpation or extinction, their roles and effectiveness in achieving long-term recovery (i.e., population self-sustainability) remain equivocal (Brown and Day 2002; Belk et al. 2008; Milot et al. 2013; Naslund and Johnsson 2014).

Quantifying the effectiveness of stocking efforts is imperative for assessing and adaptively managing these programs. Stocked individuals often suffer from low survivorship and limited recruitment (i.e., survival to reproductive maturity; Cochran-Biederman et al. 2015), which may be partially attributable to maladaptive behavioral, phenotypic, and genetic consequences associated with benign hatchery conditions or contemporary environmental conditions (Araki et al. 2007; Belk et al. 2008; Frankham 2008; Naslund and Johnsson 2014). If recruitment of stocked fishes does occur (i.e., growth to reproductive adults), repatriated individuals may respond differently to local environments compared to wild conspecifics, resulting in reduced viability of augmented populations (Chilcote 2003; Williamson et al. 2010). Because fish are often stocked as fry or juveniles, quantifying the mortality of young age-classes will be especially important for rapidly measuring the success of stocking programs.

63   Native fishes of the Colorado River basin have experienced dramatic declines over the

64   last century due to high levels of anthropogenic disturbance (Minckley and Deacon 1968; Poff et

65   al. 1997; Minckley et al. 2003; Olden et al. 2006). Extensive water development and habitat

66   alterations (Minckley and Deacon 1968; Poff et al. 1997), coupled with the introduction of over

67   60 nonnative species (Olden et al. 2006), have driven declines and prompted managers to initiate

68   hatchery augmentation efforts for several endangered species (Nesler et al. 2003; Schooley and

69   Marsh 2007; Zelasko et al. 2010).

70   The federally protected Colorado Pikeminnow *Ptychocheilus lucius* is endemic to the

71   Colorado River basin of western North America (USFWS 1967; Tyus 1991). This large-bodied,

72   piscivorous cyprinid is highly migratory, exhibiting extensive seasonal movements (Osmundson

73   et al. 1998; Durst and Franssen 2014), and utilizes a variety of habitats through ontogeny

74   (Osmundson et al. 1998). Wild populations persist in the Colorado River and Green River

75   subbasins (Colorado and Utah) upstream of Lake Powell (Utah and Arizona) in the upper

76   Colorado River basin; however, in the San Juan River (Colorado, New Mexico, and Utah), a

77   tributary of the Colorado River, annual stocking of age-0 individuals since the mid-1990s has

78   been used to repatriate the historical population (Tyus et al. 1982; Platania et al. 1991). Despite

79   these efforts, stocked fish are rarely observed 3 years after stocking; this, coupled with a life

80   history that includes delayed sexual maturation (6 years of age; Vanicek and Kramer 1969), has

81   resulted in the presence of few reproductive individuals in the river, thus limiting the

82   population's sustainability.

83   Throughout the Colorado River basin, electrofishing via boats or rafts remains a common

84   technique to monitor large-bodied endangered fishes through a capture-and-release methodology

85   (Bestgen et al. 2007; Zelasko et al. 2010; Franssen and Durst 2014; Franssen et al. 2014). A

86   fundamental assumption implicit in the usefulness of this approach, however, is that mortality

87   associated with the capture-and-release process is minimal. Furthermore, as the endangered fish

88   recovery efforts in the upper Colorado River basin (Colorado, Green, and San Juan River

89   subbasins) rely heavily on capture-and-release methods to monitor demographic parameters of

90   endangered species (e.g., Bestgen et al. 2007; Zelasko et al. 2010; Franssen and Durst 2014;

91   Franssen et al. 2014; Osmundson and White 2017), captured individuals are typically subjected

92   to additional handling procedures (e.g., live-well containment, tagging, and length and mass

93   measurements) that have the potential to negatively affect short- or long-term survival

94   (Pollock and Pine 2007). While these activities are essential for monitoring the status of

95   populations and recovery progress, their efficacy is contingent on minimizing detrimental

96   population-level effects.

97   To investigate the recruitment limitations hindering Colorado Pikeminnow stocking

98   efforts in the San Juan River, we assessed apparent survival (hereafter, "survival") and capture

99   probabilities by using recaptures of marked individuals between 2003 and 2016. Although our

100   specific aim was to quantify survival among age-classes (or age-groups), we also assessed

101   variation in survival and capture rates annually, spatially, and across individual attributes.

102   Furthermore, considering the spatially extensive and temporally intensive management and

103   monitoring activities that are implemented annually in the San Juan River, we explored potential

104   capture-related effects on the survival of Colorado Pikeminnow.

105

106   <A> Methods

107   <C> *Study System.*– The headwaters of the San Juan River emerge from the San Juan Mountains

108   of southwestern Colorado and drain approximately 99,200 km^2 of Colorado, New Mexico, Utah,

109 and Arizona before reaching Lake Powell (Carlson and Carlson 1982; Figure 1). Completion of

110 Navajo Dam (river kilometer [RKM] 365) in 1962 impounded the upper San Juan River, thereby

111 modifying the river's geomorphology and disrupting its natural flow regime. Channel

112 morphology and complexity exhibit longitudinal and lateral variation between Navajo Dam

113 and Lake Powell (RKM 0; Bliesner and Lamarra 2000; Franssen et al. 2015). The lower section

114 of the river is largely canyon-bound, while the middle reaches exhibit substantial lateral

115 complexity (channel braiding and secondary channels). The upper portion of the San Juan River

116 has been severely impacted by anthropogenic activities and is channelized throughout (Franssen

117 et al. 2015). Furthermore, declining water levels in Lake Powell have created a waterfall that

118 limits upstream movements from the lake to the river (Durst and Franssen 2014). Consequently,

119 these upstream and downstream barriers have limited the accessibility and quantity of available

120 habitats, along with altering the timing and magnitude of peak flows in the San Juan River.

121

122 <C> *Fish stocking, tagging, and sampling*.– Stocking of Colorado Pikeminnow in the San Juan

123 River was initiated in 1996, and the number of individuals stocked has been variable across years

124 (Table 1). Age-0 Colorado Pikeminnow were stocked (Southwestern Native Aquatic Resources

125 and Recovery Center, Dexter, New Mexico) between RKM 315.4 and RKM 268.1; due to their

126 small size at stocking (1996–2016 annual mean = 55 mm TL; range = 24–85 mm TL; Furr

127 2017), the fish did not receive a PIT tag (12 mm; Biomark, Inc.) until their first encounter in the

128 field. We used raft mounted electrofishing units to recapture Colorado Pikeminnow during

129 annual large-bodied fish monitoring and nonnative fish removal efforts between RKM 289.7 and

130 4.6. These sampling efforts consisted of two electrofishing rafts progressing in a downstream

131 direction, sampling both shorelines and holding captured fish in live wells until live-well

132   capacity was reached or following a maximum of 4.8 RKM, whichever occurred first. Riverwide

133   surveys for large-bodied fish were conducted annually in September or October and sampled

134   three out of every four 1.6-RKM reaches. Annual nonnative fish removal efforts were spatially

135   and temporally variable throughout the study period due to adaptive management activities

136   carried out by the U.S. Fish and Wildlife Service (USFWS) San Juan River Basin Recovery

137   Implementation Program (Table 1; Franssen et al. 2014). Captured fish were scanned for the

138   presence of a PIT tag (unmarked fish received an implanted tag), measured (TL, mm), weighed

139   (g), and returned to the river after capture.

140

141   <C> *Apparent survival and capture probabilities*.– We used a Cormack–Jolly–Seber open-

142   population model (Cormack 1964; Jolly 1965; Seber 1965) in Program MARK (White and

143   Burnham 1999) to estimate apparent survival (ϕ) and capture probability (p) of Colorado

144   Pikeminnow captured between 2003 and 2016. We restricted our analyses to those years because

145   Colorado Pikeminnow captures were highest during that time period. Encounter histories for

146   each fish were constructed from captures of PIT-tagged individuals. We treated each year as an

147   encounter interval and collapsed multiple captures of an individual within a year into a single

148   capture in an individual's encounter history.

149

150   <C> *Model structures and selection procedure*.– As our primary interest was to investigate age-

151   specific survival, we modeled ϕ and p as a function of first-encounter age (first captured at age 1,

152   2, or 3+; modeled as groups) using known length–age relationships (Durst and Franssen 2014),

153   along with the encounter date, to assign each individual to an age-group. A suite of candidate

154   models was used to test whether ϕ and p of Colorado Pikeminnow age-groups varied through

155 time and were influenced by the additive effects of first-encounter size (TL and TL^2), residual

156 weight (RW; residuals of log-transformed length–weight regression as a metric of body

157 condition), and location (RKM; Table 2). The squared TL term was included to account for non-

158 linear size effects influencing estimates of ϕ and p. For instances in which weights were not

159 recorded or in which discrepancies existed (204 [2.0%] of individuals), we assigned those

160 individuals the predicted weights estimated from the observed length–weight relationship ($\log_{10}w$

161 $= 3.054 \cdot \log_{10}[TL] - 5.289$).

162   To reduce the total number of models considered and thus reduce computational time, we

163 sequentially analyzed three sets of models (Table 2). First, we evaluated a series of time

164 structures to assess temporal variation in ϕ and p-estimates across age-groups. For both ϕ and p,

165 we modeled capture effects (*C*) over the first two time intervals with several models, including

166 constant first- and second year effects with constant (*C1 + C2*) or time-varying (*C1 + C2 + t*)

167 subsequent annual variability (i.e., capture intervals after *C1* and *C2*); time-varying first- and

168 second-year effects with constant subsequent annual variation (*C1t + C2t*); and time-varying

169 first- and second-year effects with time varying subsequent annual variability (*C1t + C2t + t*).

170 We also constructed a fully time-variant annual model without capture effects (*t*) and a constant,

171 time-invariant (.) model. Inclusion of the first and second time intervals allowed us to estimate

172 some age-specific survival and capture effects (Supplementary Table S.1 available in the online

173 version of this article); however, sample sizes precluded us from assessing successive time

174 intervals beyond the first two intervals. Furthermore, as age increased with the first and second

175 time intervals (e.g., age-1 fish progressed to age 2 across the first two capture periods), we were

176 unable to differentiate confounding effects of age and capture effects for all age-groups. All

177 possible combinations of age and time structures were evaluated, and models were ranked using

178 Akaike's information criterion adjusted for small sample sizes (AIC_c). We tested the goodness of

179 fit of the most complex model structure by using the median *c*-hat (c) procedure (Cooch and

180 White 2011). We corrected and reweighted the final model set (quasi-AIC_c [$QAIC_c$]) based on

181 the resultant c to account for a lack of fit due to overdispersion. We retained the highest-ranked

182 time structures with reasonable support (those with a $QAIC_c$ difference [$\Delta QAIC_c$] < 2.0 and an

183 Akaike weight [w_i] > 10%; Burnham and Anderson 2002); using the top model(s) for age and

184 time effects, we then evaluated the influence of the individual covariates on both φ and p (TL,

185 TL^2, RW, and RKM encountered). As covariates reflected data that were collected at an

186 individual's first encounter, all individual covariates were only applied to the first time interval.

187   To further reduce computational time when assessing covariates, we employed a

188 sequential approach to produce the most parsimonious φ and p structures (Nichols et al. 1997;

189 Zelasko et al. 2010). Using the retained time structures (see Results below), we began by

190 constructing the most complex p structure (highest-supported time structure and all individual

191 covariates), which was held constant as we increased the complexity of the φ structure by

192 successively adding covariates starting from a null model (highest-supported time structure but

193 no individual covariates). In effect, this forced most of the variability to be captured in the p

194 structure, which allowed us to better estimate the φ structure (Zelasko et al. 2010). After all

195 possible φ structures were run, we retained the highest ranking φ structures and subsequently ran

196 all possible combinations by increasing the complexity of the p structure in an identical manner.

197   In the final model set, we used the time structure and covariate model(s) with the highest

198 support to estimate capture and size (TL) effects on survival among age-groups (Table 2). To

199 evaluate putative capture effects, we fitted models allowing the first- and second-year effects to

200 vary among age-groups (*C1t* + *C2t* × AG). To estimate whether size (TL) had differential effects

201 across age-groups, we fitted models that constrained survival to be equal among age-groups

202 ($TL_{1=2=3}$) as well as models that allowed size effects to vary among age-groups (i.e., TL × age-

203 group interaction). Models that included a unique effect of TL for age-3+ fish resulted in many

204 inestimable parameters due to low sample sizes within this group; thus, we only fitted models

205 that allowed for common effects of TL for ages 2 and 3+, differing from the effect for the age-1

206 group ($TL_{1|2=3}$). To account for uncertainty in assessing the most appropriate model(s) for

207 interpretation, we used weighted model averaging based on w_i to quantify survival and capture

208 estimates as well as covariates that were present in models with reasonable support (those with

209 $\Delta QAIC_c < 2.0$ and $w_i > 10\%$). As our primary interest was in age-specific estimates, we used the

210 real survival parameters (unique estimates for each year, time interval, and age-group

211 combination) to calculate age-specific survival and capture probabilities for individuals of

212 known age and more conservatively for age-groups (i.e., ages 3+ and 4+) in which discrete ages

213 could not be identified (i.e., after the first and second time intervals).

214

215 <C> *Capture effects of age 2 Colorado Pikeminnow*.–To better understand the potential capture

216 effects on known age-2 Colorado Pikeminnow, we used a series of generalized linear mixed-

217 effects models (GLMM) to evaluate how the probability of future recapture (binary response

218 variable) varied by the age at first encounter (i.e., age-2 fish tagged the previous year and

219 recaptured the year of versus age-2 fish first captured the year of) and TL to control for size

220 effects. We built four models using the singular, additive and interactive combinations of age at

221 first encounter and TL. A fifth model (no fixed effects) was used as a null model and all models

222 featured year as a random effect with a random intercept. Models were compared using AIC_c and

223   we interpreted models with a ΔAIC_c less than 2.0 and a w_i greater than 10%. Models were fit

224   using the "lme4" package (Bates et al. 2015) in R (R Core Team 2017).

225

226   <A> Results

227   The full data set included a total of 10,365 individual Colorado Pikeminnow representing

228   11,401 captures between 2003 and 2016 (Table 1). Captures tended to be higher in the late

229   summer and early fall compared to other seasons (Figure 2), and individuals were most often

230   first encountered as age-1 ($n = 5,413$) or age-2 ($n = 4,400$) fish, with substantially fewer

231   individuals represented in the age-3+ group ($n = 552$). The majority of individuals were

232   encountered once (92%), few were captured twice (7%), and individuals captured three or more

233   times were rare (1%; range = 3–6 encounters). Size at first encounter ranged from 107 to 620

234   mm TL and varied minimally among years within age-groups, with the exception of age-3+

235   individuals (Figure 3). No apparent trends were observed among years or age-groups in RW.

236   Spatially, individuals were encountered along the entire sampled reach; however, there was a

237   slight trend of age-1 individuals captured at more upstream locations (Figure 3).

238

239   <B> Model Selection

240   Goodness-of-fit testing indicated slight overdispersion of the data ($c = 1:36$, SE = 0.004;

241   1,000 simulations); thus, the final candidate model set was adjusted prior to interpretation. Model

242   selection of candidate time structures (i.e., no covariates) resulted in two top-ranking models

243   ($\Delta QAIC_c < 2.0$ and $w_i > 10\%$) that differed in their p structure (not shown). The highest-ranking

244   time structure ($w_i = 0.47$) featured annual variation over the first two time intervals and in

245   subsequent time intervals ($C1t + C2t + t$) for both ϕ and p. The second model ($\Delta QAIC_c = 1.86$;

246    $w_i = 0.18$) differed only in the p structure and featured annual variation over the first two time

247   intervals but a constant p for all subsequent time intervals ($C1t + C2t$). The final model set

248   (covariates and age-group interactions included) resulted in three models (cumulative $w_i = 0.50$)

249   with reasonable support that included TL and TL^2 (ϕ), RW (ϕ and p), RKM (p), and the two

250   competing time structures (Table 3). Only one covariate differed among the top models (RW was

251   included in the ϕ portion of the third-best model); thus, we interpreted the parameter estimates

252   from the more complex third model. However, qualitative comparison with the other two

253   competing models resulted in a similar directionality and magnitude of model parameters.

254

255   <B> Apparent Survival Estimates

256   The most complex model was the third model, which resulted in 25 estimable parameters

257   for apparent survival (Table 4). Survival parameters included an intercept (estimating survival

258   for age-3+ individuals in 2016 subsequent to the first two time intervals); first time interval ($C1t$)

259   and second time interval ($C2t$) effects across age-groups; annual variation; TL and TL^2

260   interactions among age-groups; and RW. Estimated survival was similar among the three age-

261   groups and was generally consistent throughout the study period, with the exception of 2007 and

262   2012, which exhibited substantially lower survival. First-encounter size (TL) had a positive

263   effect on first-year survival rates of Colorado Pikeminnow; however, the extent of this effect

264   varied by age-group (Table 4). The top models all featured a common size effect for age-2 and

265   age-3+ groups that was different from the effect for the age-1 group ($TL_{1|2=3}$). Size effects on

266   first-year survival were minimal for age-1 fish; however, TL^2 had a strong and positive effect on

267   survival for the age-2 and age-3+ groups, indicating a non-linear effect of size on first-year

268   survival (Figure 4). Estimated effects of RW on survival were negligible (Table 4).

269   In total, 108 real survival parameters were possible; of these, 21 were inestimable due to

270 low capture probabilities or small sample sizes (Figure 5). Age-specific estimates for individuals

271 of known age revealed that survival was equal to or less than 0.25 during the first 3 years post-

272 stocking (0.19, 0.25, and 0.22 for ages 1, 2, and 3, respectively). Survival increased for age-4

273 individuals (0.53); however, confidence intervals overlapped those of younger age-classes (Table

274 5). Age-groups exhibited a similar trend, as mean survival was 0.17 and 0.60 for age-3+ and age-

275 4+ fish, respectively (Table 5).

276

277 <B> Capture Effects

278   Capture effects were confounded with age for most age-groups (e.g., our only survival

279 estimates for age-1 fish came from captured individuals); however, we were able to evaluate the

280 effect of capture for individuals that were of known age 2. These effects were interpreted using

281 the second-year survival estimates on the age-1 group ($C2t_{\text{Age 1}}$ in Table 4) and the first-year

282 effects from the age-2 group ($C1t_{\text{Age 2}}$). No individuals from the age-1 group were recaptured

283 after the first two capture periods in 2005 and 2006; thus, we could only evaluate capture effects

284 from 2007 to 2016. On average, survival was approximately 50% lower (a 0.17 mean reduction

285 in survival) for age-2 fish in the first year after capture compared to age-1 fish in their second-

286 year after capture (Figure 6), suggesting that capture and handling effects measurably reduced

287 survival.

288   We retained two GLMMs (logistic regression) with reasonable support ($\Delta\text{AIC}_c < 2.0$; w_i

289 $> 10\%$) predicting the recapture probability of known age-2 fish. The highest-ranked model

290 featured the additive effects of first-encounter age and TL ($\Delta\text{AIC}_c = 0.0$; $w_i = 0.61$). Individuals

291 that were first handled at age 1 displayed significantly higher recapture probabilities compared to

292　individuals that were first captured at age 2 (β = -0.61, SE = 0.18), and TL was positively related

293　to recapture probability (β = 0.75, SE = 0.33; Figure 7). The second interpretable model (ΔAIC_c

294　= 1.8; w_i = 0.24) featured only first-encounter age and similarly indicated that fish first captured

295　at age 1 displayed higher recapture probabilities than individuals that were first captured at age 2

296　(β = -0.55, SE = 0.18).

297

298　<B> Capture Probability Estimates

299　　　　Capture probability was modeled with 19 parameters (Table 6) that included the same

300　time-specific parameters (first- and second-year effects, annual variation) as those modeled for

301　survival (but did not differ among age-groups) and also included RW and RKM. Capture

302　probabilities were similar across age-groups and were consistent across years and among time

303　intervals (Table 6). Mean capture probabilities averaged between 0.34 and 0.39 for the first two

304　years postcapture (*C1t* and *C2t*) and 0.31 in subsequent time intervals. Residual weight and

305　RKM were negatively related to capture probability (Table 6), indicating more robust fish were

306　less likely to be encountered and capture rates were higher in the downstream, canyon-bound

307　reaches of the river. Age-specific estimates derived from real capture probability parameters

308　(same as those modeled and retained for ϕ) resulted in similar capture rates for individuals of

309　known ages and age-groups (Table 5; Figure 8).

310

311　<A> Discussion

312　　　　Our results indicated persistently low survivorship of stocked juvenile Colorado

313　Pikeminnow through the first 3 years post-stocking, which has limited the numbers of recruited

314　adults in the San Juan River. As far as we know, these are the first empirically based survival

315 estimates for these age-classes of Colorado Pikeminnow. Although size disparities limit

316 comparisons of survival estimates with other studies (Osmundson and Burnham 1998; Bestgen et

317 al. 2007), some comparisons within overlapping portions of the size distributions were possible.

318 At the overlapping sizes of fish (~350 mm TL), survival of Colorado Pikeminnow in the San

319 Juan River was approximately 25% lower than estimates (2000–2003) for those in the Green

320 River subbasin of the Colorado River basin (estimated from Figure 4 in Bestgen et al. 2007).

321 However, as individuals reached 450 mm and larger sizes, survival estimates were comparable

322 between the basins, further suggesting relatively low juvenile survival in the San Juan River.

323 Although temporal variability in recruitment may be expected for long-lived fishes (Osmundson

324 and White 2017), estimated survival across age-groups of stocked Colorado Pikeminnow in the

325 San Juan River has remained consistent throughout the last two decades. Given these results,

326 identifying and ameliorating the factors that limit recruitment of Colorado Pikeminnow across

327 the Colorado River basin will constitute a major challenge for managers to secure recovery of the

328 species.

329   Size at first encounter had interactive effects with age on the survival of Colorado

330 Pikeminnow. First-year post-capture survival was influenced by size at encounter, and this was

331 especially apparent for larger individuals. As size generally correlates with increased survival of

332 stocked fish (Justice et al. 2009; Zelasko et al. 2010), the relatively constant survival rates across

333 ages 1–3 were surprising given that Colorado Pikeminnow stocked into the San Juan River tend

334 to be longer at a given age compared to their wild counterparts in the upper Colorado River basin

335 (Durst and Franssen 2014). A possible explanation may be related to deleterious capture effects

336 that appeared to intensify for moderately sized individuals. Although capture effects were

337 confounded with age for most age-group comparisons, we were able to directly test these effects

15

338   for known age-2 individuals. Survival was substantially lower for fish that were first captured at

339   age 2 compared to age-2 fish that were first handled at age 1. In addition, lower survival of age-

340   3+ fish after the first year of capture compared to age-1 and age-2 fish provides further evidence

341   of seemingly detrimental capture effects. Survival rebounded during the second year after

342   capture for the age-1 and age-3+ groups; however, capture effects appeared to linger for

343   individuals that were initially captured at age 2, suggesting that this size-class/age-class was the

344   most vulnerable to deleterious capture effects. Although the exact mechanisms contributing to

345   these capture effects are unclear, the results suggest that factors associated with capture stress,

346   such as electrofishing (Dalbey et al. 1996; Nielsen 1998), handling/tagging (Bateman and

347   Gresswell 2006; Ficke et al. 2012), live-well housing (Schramm et al. 2006), and environmental

348   conditions (Schramm et al. 2010), have the potential to affect the survival of Colorado

349   Pikeminnow in the San Juan River.

350   Bestgen et al. (2007) found no evidence to support increased mortality associated with

351   electrofishing and capture of Colorado Pikeminnow in the Green River subbasin. Our data also

352   indicated that lower survival rates in the San Juan River were not limited to electrofishing, and

353   the intensity and timing of sampling activities in the San Juan River could explain some of the

354   discrepancies in potential capture effects between studies. First, annual sampling efforts in the

355   San Juan River are spatially extensive (78% of the river sampled) and intensive (multiple

356   seasonal passes), reflected in the relatively high capture probabilities compared to those reported

357   in other studies (Osmundson and Burnham 1998; Bestgen et al. 2007). Perhaps more

358   importantly, our age-specific capture probabilities suggest that a large proportion of the

359   population is likely being handled between ages 1 and 3, ages during which minimal increases in

360   survival were observed, indicating that the survival results were more likely related to stress

361 associated with the timing of handling activities. The higher return rates of age-2 Colorado

362 Pikeminnow first handled at age 1 provide evidence that these effects are not exclusively related

363 to electrofishing, as these individuals were exposed to repeated electrofishing and handling

364 effects in successive years. Because the observed capture effects were most prominent after an

365 individual's first encounter, we cannot rule out effects related to PIT tag implantation. However,

366 we think these effects have likely been intensified by the magnitude and timing (seasonality) of

367 annual sampling efforts within the San Juan River. In contrast to the targeted spring sampling

368 utilized in the Green River subbasin (Bestgen et al. 2007), Colorado Pikeminnow are captured

369 nearly year-round in the San Juan River, with a disproportionately higher number of individuals

370 captured throughout the summer and fall. Water (and live-well) temperatures are considerably

371 warmer during these months, which could result in increased physiological stress and mortality

372 (Schramm et al. 2010). Although these capture-related effects appear to be limiting the survival

373 of stocked Colorado Pikeminnow in the San Juan River, identifying the relative impact of the

374 individual capture components, and mitigating their effects, will likely necessitate future

375 evaluations.

376 In addition to capture effects, apparent survival of juvenile Colorado Pikeminnow was

377 likely affected by individuals leaving the study area. Long-distance seasonal movements (Tyus

378 and McAda 1984; Tyus 1991; Durst and Franssen 2014) and tributary usage have been

379 documented (Fresques et al. 2013; Cathcart et al. 2015). Substantial downstream movements in

380 the San Juan River are especially problematic because individuals traversing the large waterfall

381 at the confluence of Lake Powell fare poorly—and, more importantly, are likely restricted from

382 returning to the river (Durst and Francis 2016; Francis et al. 2017). Although emigration rates are

383 unknown, substantial downstream winter movements and captures of individuals in Lake Powell

384　(Durst and Francis 2016) indicate that a considerable proportion of stocked fish may be leaving

385　the system (Durst and Franssen 2014). Similarly, it is conceivable that individuals may be

386　actively avoiding the electrofishing gear during the first time interval after capture. Although we

387　think this unlikely based on the relatively high and consistent capture probabilities, fish in the

388　San Juan River are exposed to a considerable amount of annual electrofishing effort, and

389　behavioral avoidance of the electrofishing rafts is possible. A number of stationary PIT antennas

390　is currently positioned throughout the upper reaches of the San Juan River and tributaries and

391　may help to provide insight into the extent of this behavior.

392

393　<B> Future Directions and Management Implications

394　　　Survival showed no appreciable increases until age 4, indicating that the size or age of

395　fish greater than age 3 coincided with release from an apparent constraint on survival. Our age-

396　specific capture probabilities indicate that a large proportion of stocked Colorado Pikeminnow

397　are likely being subjected to capture, tagging, and handling stress during their first 3 years in the

398　river. Although we acknowledge that the exact mechanisms driving the observed capture effects

399　are currently unclear, these effects do appear to be contributing to the consistently low survival

400　of age-1–3 Colorado Pikeminnow in the San Juan River. As a first step to reduce capture-related

401　stress, the USFWS San Juan River Basin Recovery Implementation Program has ceased the

402　capture and handling of Colorado Pikeminnow during warmer months and will rely solely on

403　annual large-bodied monitoring efforts to obtain demographic information. While this will

404　effectively reduce future capture probability estimates and the number of tagged fish in the river,

405　we are optimistic that reducing the handling frequency will boost juvenile survival. As field-

406　based monitoring activities often preclude the ability to use traditional control treatments

407   (Pollock and Pine 2007), differentiating the relative contributions of the individual components

408   that constitute a capture and handling event will likely rely on future experimental approaches.

409   Depending on the magnitude of capture effects at the population level, we recognize that

410   our ability to estimate the true survival of Colorado Pikeminnow stocked into the San Juan River

411   may be obscured. Until we can identify and minimize these detrimental capture effects, efforts to

412   determine the underlying factors responsible for the initial population declines are limited.

413   Anthropogenic alterations have resulted in substantial biotic (e.g., nonnative predators; Franssen

414   et al. 2014; Pennock et al. 2018) and abiotic (e.g., altered flow regime; Propst and Gido 2004;

415   Gido and Propst 2012) changes that have modified the quality and availability of habitats in the

416   San Juan River (Franssen et al. 2015); however, any confounding capture-induced mortality

417   should similarly be minimized. Furthermore, it is unclear whether naturally spawned Colorado

418   Pikeminnow in the San Juan River will have similar survival rates compared to stocked

419   individuals, but a spawning adult population will be requisite before we can make this

420   assessment. Augmentation efforts have resulted in a relatively small number of adult Colorado

421   Pikeminnow in the San Juan River (Schleicher 2017), and natural levels of spawning and

422   recruitment are minimal and infrequent (Farrington et al. 2017; Zeigler and Ruhl 2017).

423   Therefore, our ability to boost adult population sizes in the San Juan River is limited to

424   improving the survival of stocked Colorado Pikeminnow, at least until natural recruitment

425   becomes more robust. Nonetheless, reliance on hatchery supplementation will not result in the

426   species' recovery if the underlying factors responsible for low natural recruitment—whether the

427   mechanisms are anthropogenic or natural—are not ameliorated. Although hatchery-reared

428   individuals are often required to repatriate extirpated populations, difficult questions remain

429   about the conflict between the necessity of stocking to bolster numbers and the potential

430 deleterious effects of continued augmentation and monitoring activities focused on recovering

431 populations.

432

433 <A> Acknowledgments

443

444 <A> References

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632

Table 1. The numbers of age-0 Colorado Pikeminnow stocked annually since 1996 and the number of individuals first encountered in each age-group during 2003 and 2015 used to estimate apparent survival and capture probabilities. The proportion of individuals recaptured in any subsequent year are in parentheses. Annual river-wide electrofishing effort (hours) are presented in the final column.

Year	Stocked	Age 1	Age 2	Age 3+	Sampling Effort (hrs)
1996	100,000	—	—	—	—
1997	116,878	—	—	—	—
1998	10,571	—	—	—	—
1999	500,000	—	—	—	—
2000	105,000	—	—	—	—
2001	—	—	—	—	—
2002	210,364	—	—	—	—
2003	175,928	73 (0.05)	1 (0)	3 (0.33)	616.2
2004	280,000	148 (0.03)	119 (0.02)	1 (1.00)	624.2
2005	302,270	140 (0.04)	219 (0.04)	12 (0.08)	579.9
2006	313,854	388 (0.03)	176 (0.08)	42 (0.02)	617.2
2007	475,790	266 (0.10)	124 (0.09)	14 (0.21)	506.1
2008	270,234	381 (0.09)	205 (0.20)	31 (0.23)	1,199.3
2009	468,000	890 (0.13)	449 (0.12)	36 (0.14)	1,256.6
2010	214,470*	1,034 (0.09)	1,053 (0.13)	36 (0.31)	1,166.2
2011	426,588	545 (0.05)	871 (0.02)	177 (0.04)	1,180.4
2012	395,640	648 (0.06)	439 (0.07)	38 (0.13)	1,090.0
2013	439,264	415 (0.07)	352 (0.05)	59 (0.08)	1,073.5
2014	393,442	193 (0.11)	191 (0.16)	39 (0.28)	1235.3
2015	402,087	302 (0.06)	201 (0.10)	64 (0.09)	1110.3
2016	432,443	—	—	—	842.5

* overwintered in hatchery and released in early 2011.

639 Table 2. Model structures used to test hypotheses related to age, time, individual covariates and capture effects on survival and

640 recapture probabilities of Colorado pikeminnow in the San Juan River. *C1(t)* and *C2(t)* represent constant (or annual) variation over

641 the first two time intervals (capture effects), respectively, and *t* represents annual time variation in subsequent time intervals. The

642 highest ranking time structure models were then used as the base models to estimate covariate effects. Individual covariates included

643 total length (TL), residual weight (RW), and river kilometer (RKM) at first encounter. Covariate models featuring TL were also fit

644 with a separate model with the additive TL^2 term ($TL+TL^2$). Capture and size effects were only evaluated on survival parameters

645 using the highest ranking covariate models.

Time structure	Covariates	Capture and size (TL) survival effects
1) No time variation (.)	1) Null (time only)	1) Capture effects differ by age-group
2) Constant time variation in first two time intervals; constant subsequent time variation (*C1+C2*)	2) TL	(*C1(t)+C2(t)*×AG); and size effects equal across age-groups ($TL_{(1=2=3+)}$)
3) Annual time variation in first two time intervals constant subsequent time variation (*C1t+C2t*)	3) RW 4) RKM	2) Capture effects differ by age-group (*C1(t)+C2(t)*×AG); and size effects
	5) TL+RW	different for age-1 group and equal for
4) Constant time variation in first two time intervals; subsequent annual time variation (*C1+C2+t*)	6) TL+RKM 7) RW+RKM	age-groups 2 and 3+ ($TL_{(1 \mid 2=3+)}$)
5) Annual time variation in first two time intervals subsequent annual time variation (*C1t+C2t+t*)	8) TL+RW+RKM	
6) Annual time variation (*t*)		

646

647 Table 3. Cormack-Jolly-Seber open population models used to estimate apparent survival (ϕ) and capture probabilities (p) of Colorado

648 Pikeminnow captured in the San Juan River between 2003 and 2016. The top ten models ranked by quasi Akaike's Information

649 Criterion adjusted for small samples sizes (QAIC$_c$; $\hat{c}$ = 1.36), which accounts for overdispersion of the data, are presented. Models

650 with ΔQAIC$_c$ <2.0 and w_i >10% were interpreted. Model parameters included first and second year variation over time varying by

651 age-groups ($C1t+C2t \times AG$), subsequent time variation (t), total length (TL and TL^2), residual weight (RW) and river kilometer (RKM)

652 at first encounter.

653

Model	QAIC$_c$	ΔQAIC$_c$	w_i	Model Likelihood	K	Deviance
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}$) p($C1t+C2t+$RW$+$RKM)	5684.14	0.00	0.23	1.00	42	5599.82
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}$) p($C1t+C2t+t+$RW$+$RKM)	5684.92	0.78	0.16	0.68	41	5602.61
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}+$RW) p($C1t+C2t+$RW$+$RKM)	5685.67	1.53	0.11	0.46	43	5599.33
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}+$RKM) p($C1t+C2t+$RW$+$RKM)	5685.94	1.81	0.09	0.41	43	5599.61
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}+$RKM) p($C1t+C2t+t+$RKM)	5685.99	1.85	0.09	0.40	41	5603.69
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}+$RW) p($C1t+C2t+t+$RW$+$RKM)	5686.44	2.30	0.07	0.32	42	5602.12
ϕ($C1t+C2t \times AG+t+$TL$_{(1\,|\,2=3+)}+$TL$^2_{(1\,|\,2=3+)}+$RKM) p($C1t+C2t+t+$RW$+$RKM)	5686.93	2.80	0.06	0.25	42	5602.61
ϕ($C1t+C2t \times AG+t+$TL$_{(1=2=3+)}+$TL$^2_{(1=2=3+)}$) p($C1t+C2t+$RW$+$RKM)	5687.29	3.15	0.05	0.21	40	5607.00
ϕ($C1t+C2t \times AG+t+$TL$_{(1=2=3+)}+$TL$^2_{(1=2=3+)}$) p($C1t+C2t +t+$RW$+$RKM)	5688.12	3.98	0.03	0.14	39	5609.84
ϕ($C1t+C2t \times AG+t+$TL$_{(1=2=3+)}+$TL$^2_{(1=2=3+)}+$RKM) p($C1t+C2t+t+$RKM)	5688.39	4.25	0.03	0.12	39	5610.11

654

655 Table 4. Parameter estimates, standard error, lower and upper 95% CI used to predict apparent

656 survival (ϕ). *C1t* and *C2t* indicate annual variability over the first and second time intervals,

657 respectively. All parameters are relative to Age 3+ Colorado Pikeminnow in 2016. Estimates

658 reference the most complex model receiving reasonable support in Table 3.

Parameter	Beta	SE	Lower CI	Upper CI
Intercept	5.020	3.557	-1.952	11.993
Age 1	-4.847	3.448	-11.605	1.912
Age 2	-3.463	3.455	-10.236	3.310
$C1t_{Age\ 1}$	-1.089	0.352	-1.780	-0.399
$C2t_{Age\ 1}$	-0.231	0.440	-1.092	0.631
$C1t_{Age\ 2}$	-2.651	0.321	-3.280	-2.022
$C2t_{Age\ 2}$	-2.293	0.390	-3.058	-1.528
$C1t_{Age\ 3+}$	-6.968	3.471	-13.771	-0.164
$C2t_{Age\ 3+}$	-4.346	3.599	-11.400	2.707
2004	-0.171	1.411	-2.936	2.595
2005	-1.444	0.936	-3.278	0.391
2006	-1.079	0.783	-2.613	0.455
2007	-1.367	0.656	-2.653	-0.081
2008	-0.215	0.642	-1.473	1.042
2009	-0.302	0.609	-1.495	0.891
2010	-0.120	0.608	-1.312	1.072
2011	-0.427	0.590	-1.583	0.728
2012	-1.585	0.608	-2.777	-0.393
2013	-0.701	0.625	-1.927	0.525
2014	-0.832	0.643	-2.092	0.428
2015	0.190	0.645	-1.075	1.455
$TL_{Age\ 1}$	-0.361	0.522	-1.385	0.663
$TL^2_{Age\ 1}$	-0.678	0.447	-1.554	0.198
$TL_{Age\ 2=3+}$	0.016	0.149	-0.275	0.308
$TL^2_{Age\ 2=3+}$	0.155	0.053	0.051	0.258
RW	0.058	0.074	-0.087	0.202

659

660   Table 5. Mean age-specific survival estimates (ϕ) and capture probabilities (p) of Colorado

661   Pikeminnow during 2003-2016. Values in parentheses represent 95% CIs around each age-

662   specific estimate.

	Apparent Survival	Capture Probability
Known age		
1	0.19 (0.10-0.37)	0.31 (0.16-0.55)
2	0.25 (0.15-0.39)	0.37 (0.21-0.60)
3	0.22 (0.12-0.36)	0.42 (0.24-0.63)
4	0.53 (0.33-0.72)	0.42 (0.19-0.68)
Age-group		
3+	0.17 (0.09-0.32)	0.32 (0.17-0.56)
4+	0.60 (0.39-0.79)	0.35 (0.20-0.55)

663

664   Table 6. Parameter estimates, standard error, lower and upper 95% CI for detection probability

665   (p). *C1t* and *C2t* indicate annual variability over the first and second time intervals, respectively.

666   All parameters are relative to Age 3+ Colorado Pikeminnow in 2016. Estimates reference the

667   most complex model receiving reasonable support in Table 3.

Parameter	Beta	SE	Lower CI	Upper CI
Intercept	-0.965	0.234	-1.424	-0.506
Age 1	-0.264	0.310	-0.872	0.344
Age 2	0.106	0.268	-0.420	0.631
C1t	0.244	0.617	-0.966	1.453
C2t	0.261	0.608	-0.931	1.452
2004	-0.776	1.400	-3.520	1.967
2005	-0.916	1.140	-3.150	1.317
2006	-0.521	0.940	-2.364	1.321
2007	0.580	0.787	-0.962	2.122
2008	-0.084	0.700	-1.455	1.287
2009	1.001	0.673	-0.319	2.321
2010	0.266	0.650	-1.008	1.539
2011	1.011	0.638	-0.240	2.262
2012	0.021	0.665	-1.282	1.324
2013	0.154	0.674	-1.167	1.475
2014	0.152	0.708	-1.237	1.540
2015	0.119	0.658	-1.171	1.409
RW	-0.226	0.115	-0.450	-0.001
RKM	-0.336	0.102	-0.535	-0.136

668

669 List of Figures

670 Figure 1. Map of the San Juan River where apparent survival (φ) and capture probabilities (p)

671 were assessed for stocked Colorado Pikeminnow. RKM 0 denotes the waterfall at the confluence

672 of Lake Powell, RKM 289.7 designates the upstream boundary of the sampling reach and Navajo

673 Dam exists at RKM 365. The shaded region between RKM 315.4 and 268.1 represents the reach

674 of stocking during 2003-2016.

675

676 Figure 2. Monthly total first encounter captures of Colorado Pikeminnow (bars) and mean (±1

677 SD) temperature (°C; symbols) between 2003 and 2016. Temperature data were obtained from

678 the San Juan River USGS gage station 09379500 near Bluff, UT.

679

680 Figure 3. Annual summary plots of individual first encounter covariates (TL, residual weight,

681 river kilometer; columns) across age-groups (rows). Box plots show medians (vertical lines),

682 25th-75th percentiles (boxes), 10th-90th percentiles (whiskers), and 5th and 95th percentiles (dots).

683 Sample sizes are reported in Table 2.

684

685 Figure 4. Relationship between apparent survival (φ) and first encounter total length (TL, mm) of

686 age 1 (107 – 205 mm) and age 2 and 3+ (209-620 mm) Colorado Pikeminnow averaged (± 95%

687 CI) across years. The break in the lines separates age 1 from ages 2 and 3+.

688

689 Figure 5. Real survival parameters (φ) across study years and survival time intervals (panels)

690 used to calculate age-specific survival estimates for Colorado Pikeminnow (reported in Table 5).

691 Survival intervals included the first time interval (upper panel), second time interval (middle

36

692 panel) and subsequent time intervals (post first or second time intervals, lower panel; see Table

693 S1). Fish are shaded according to known age (closed symbols) and age-groups (open symbols).

694 Some parameters could not be estimated due to low capture probabilities or sample sizes.

695

696 Figure 6. Survival parameters (ϕ) used to assess capture effects of age 2 fish. For this age-group,

697 survival was, on average, 50% lower the for individuals first encountered at age 2 (closed

698 symbols) compared to the fish that were first encountered at age 1 (grey symbols).

699

700 Figure 7. Relationship between total length (TL, mm) and probability of future recapture ($\pm$ 95%

701 CI) for Colorado Pikeminnow first captured as age 1 (grey lines; with subsequent capture as age

702 2) and individuals first captured as age 2 (black lines).

703

704 Figure 8. Real capture probabilities (p) across study years and time intervals (panels) used to

705 calculate age-specific capture probabilities for Colorado Pikeminnow. Time intervals included

706 the first time interval (upper panel), second time interval (middle panel) and subsequent time

707 intervals (post first or second time intervals, lower panel). Fish are shaded according to known

708 age (closed symbols) and age-groups (open symbols).
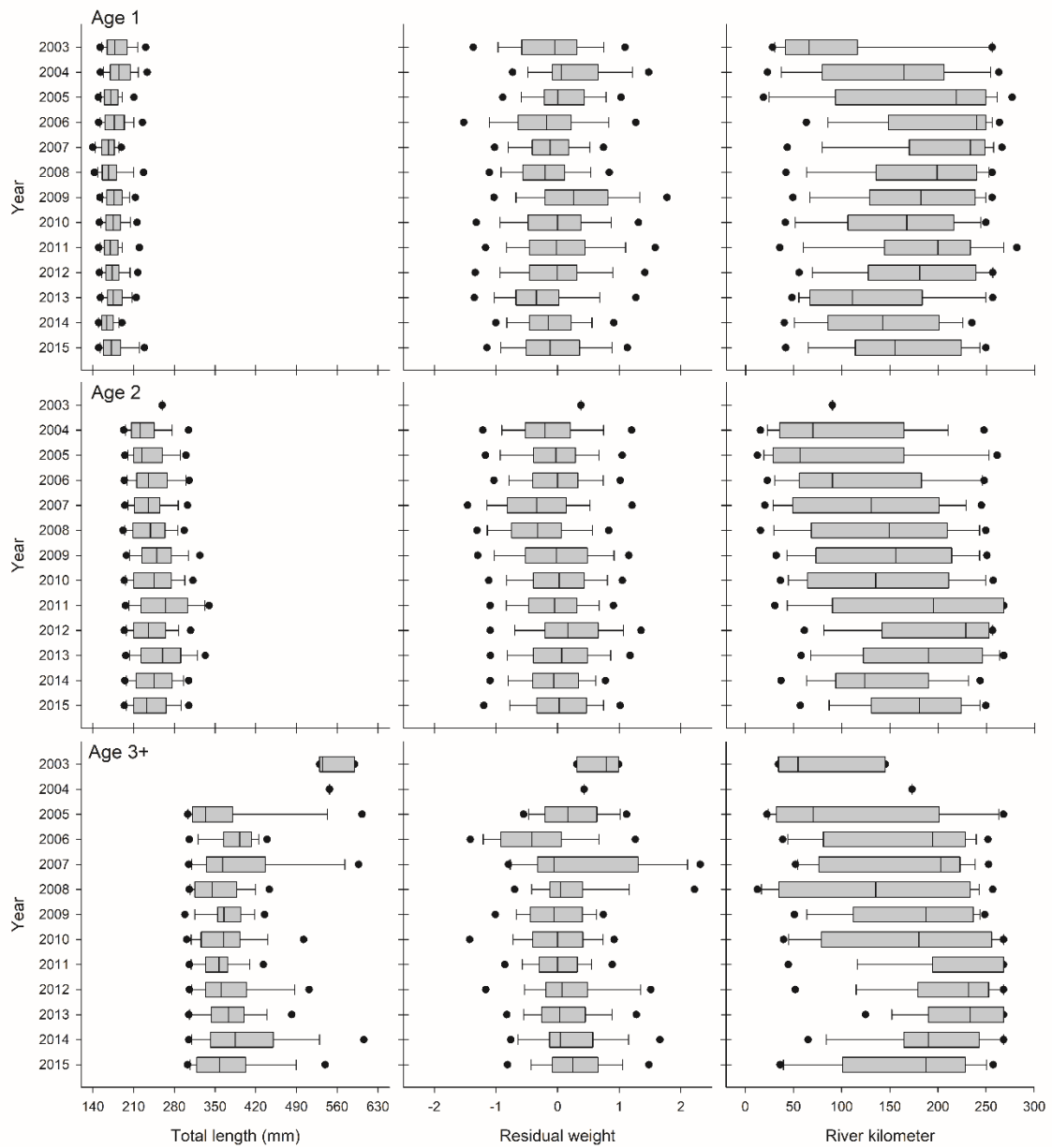
709   Fig. 1.
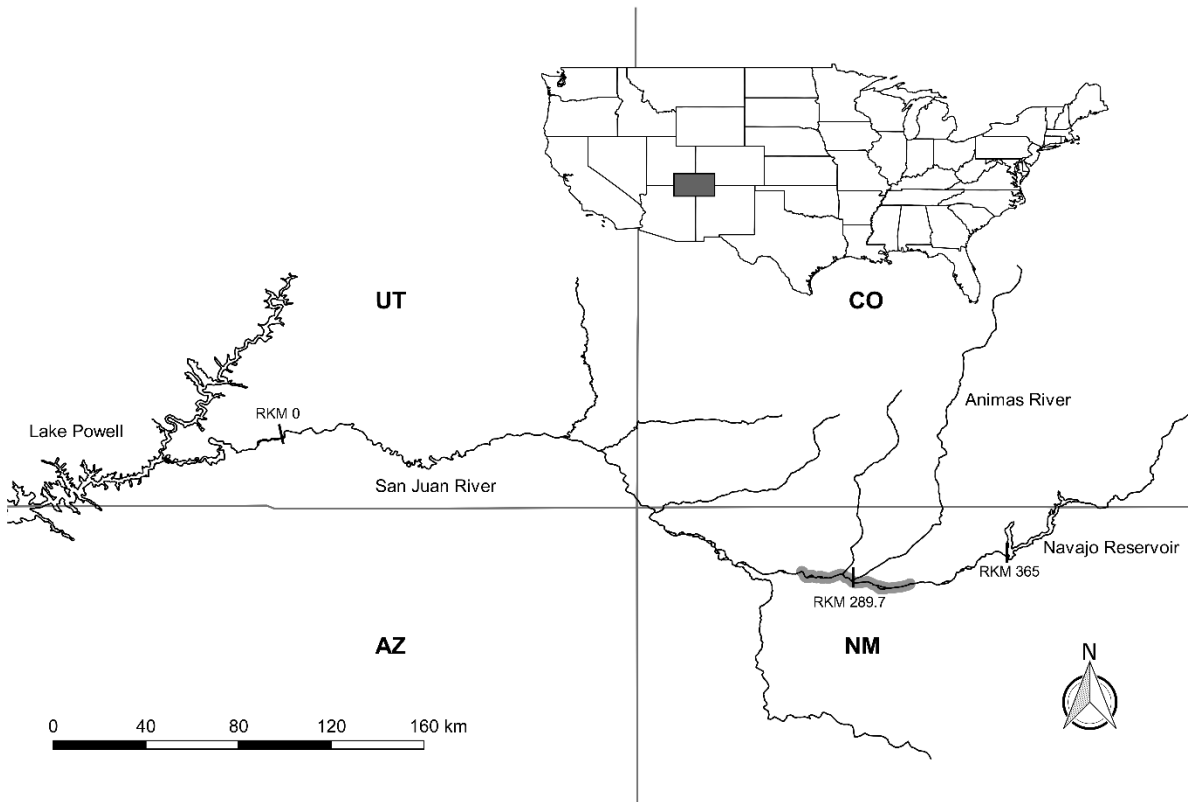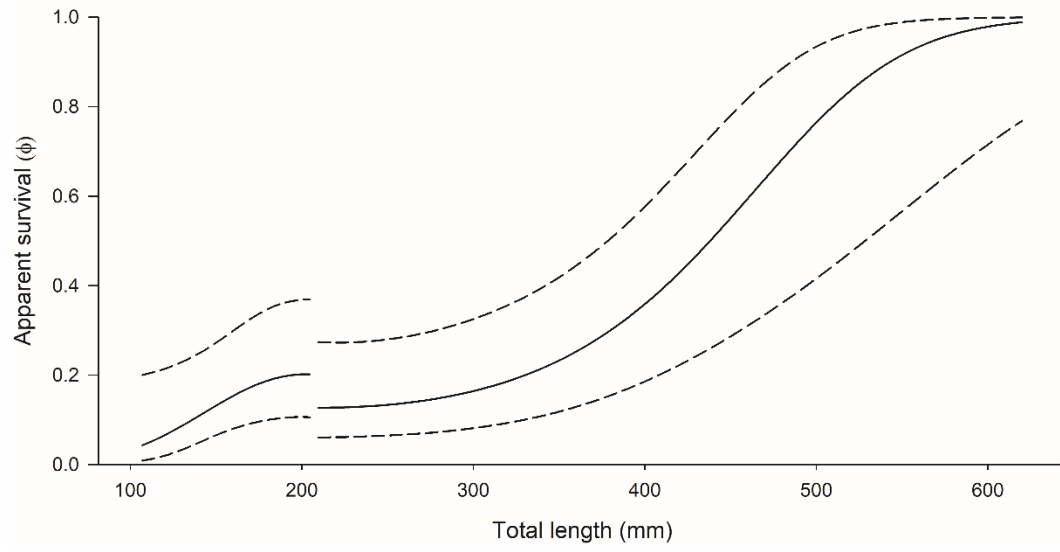

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712   Fig. 2.
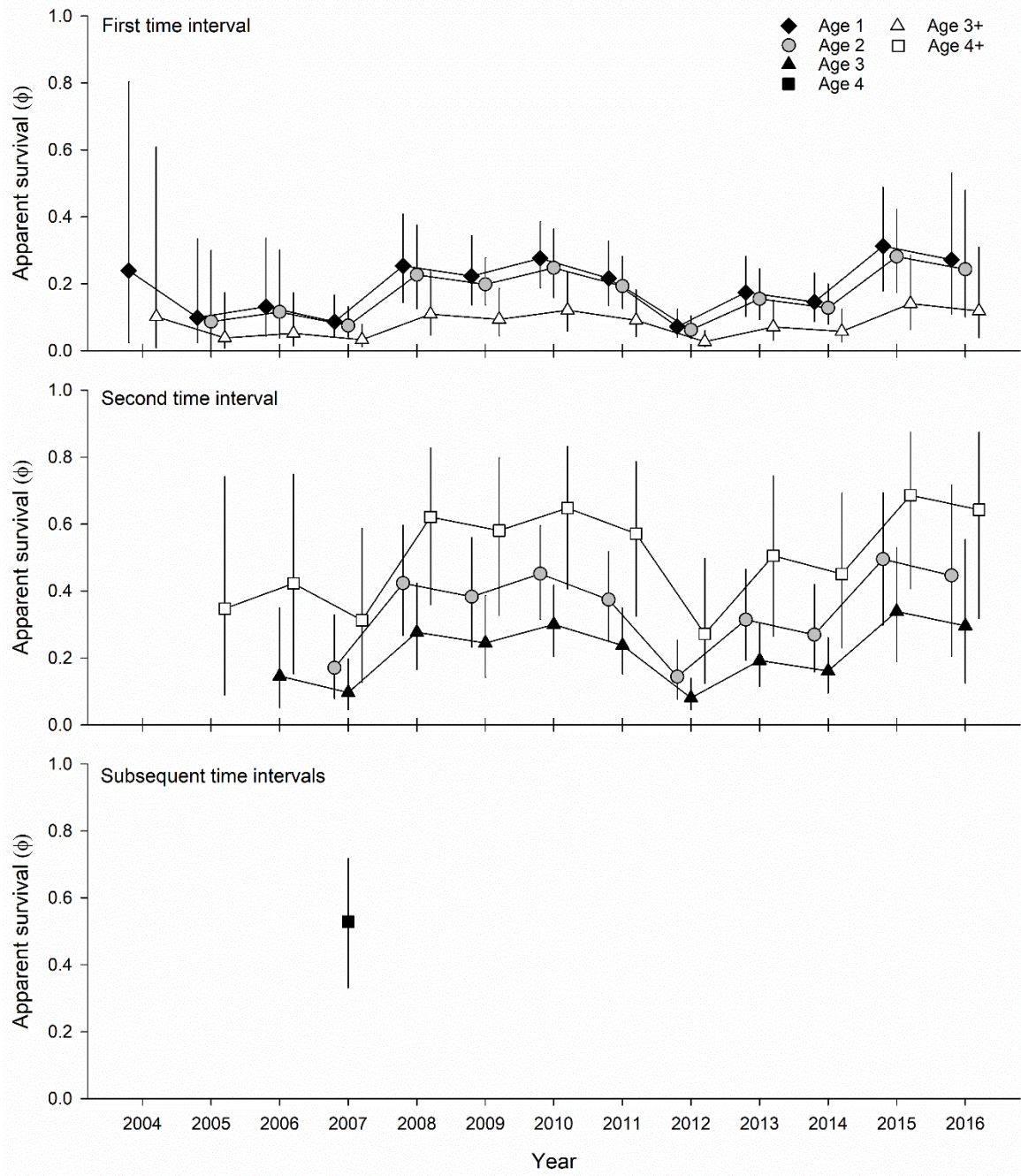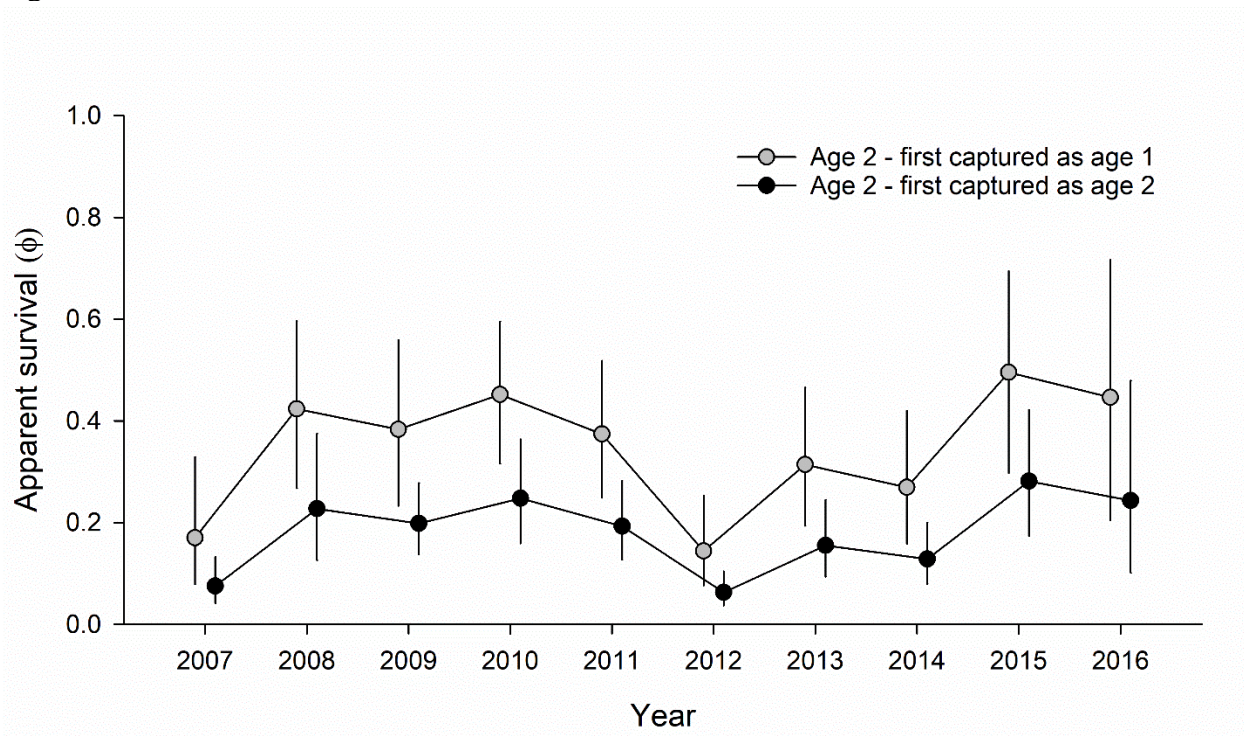

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714   Fig. 3.

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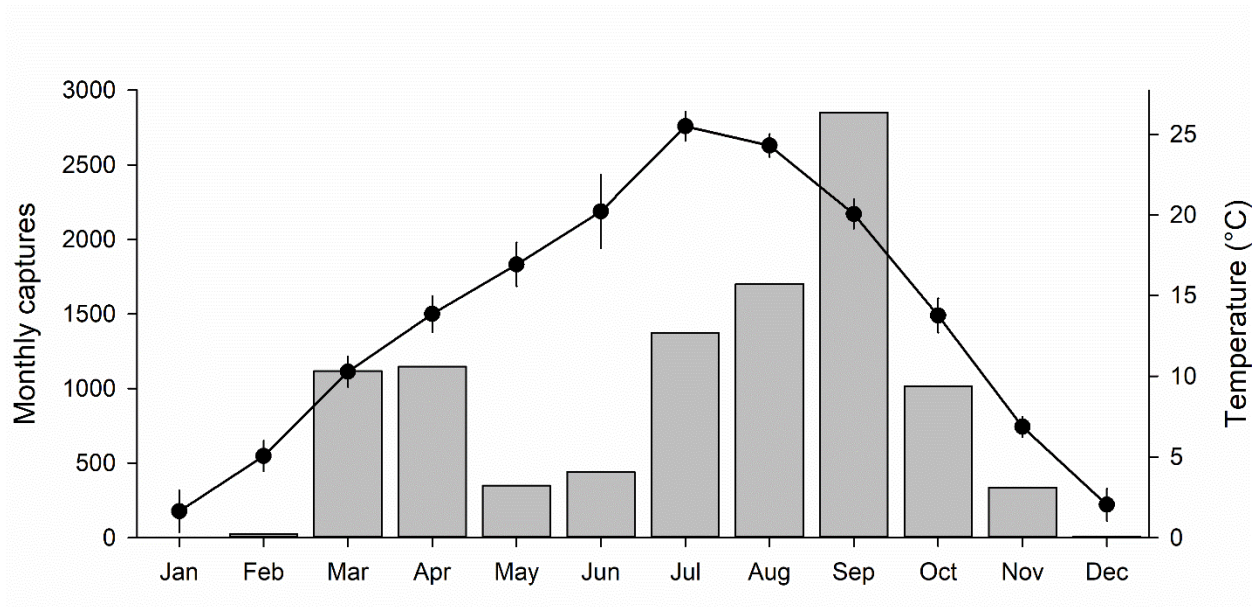
716   Fig. 4.

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718   Fig. 5.
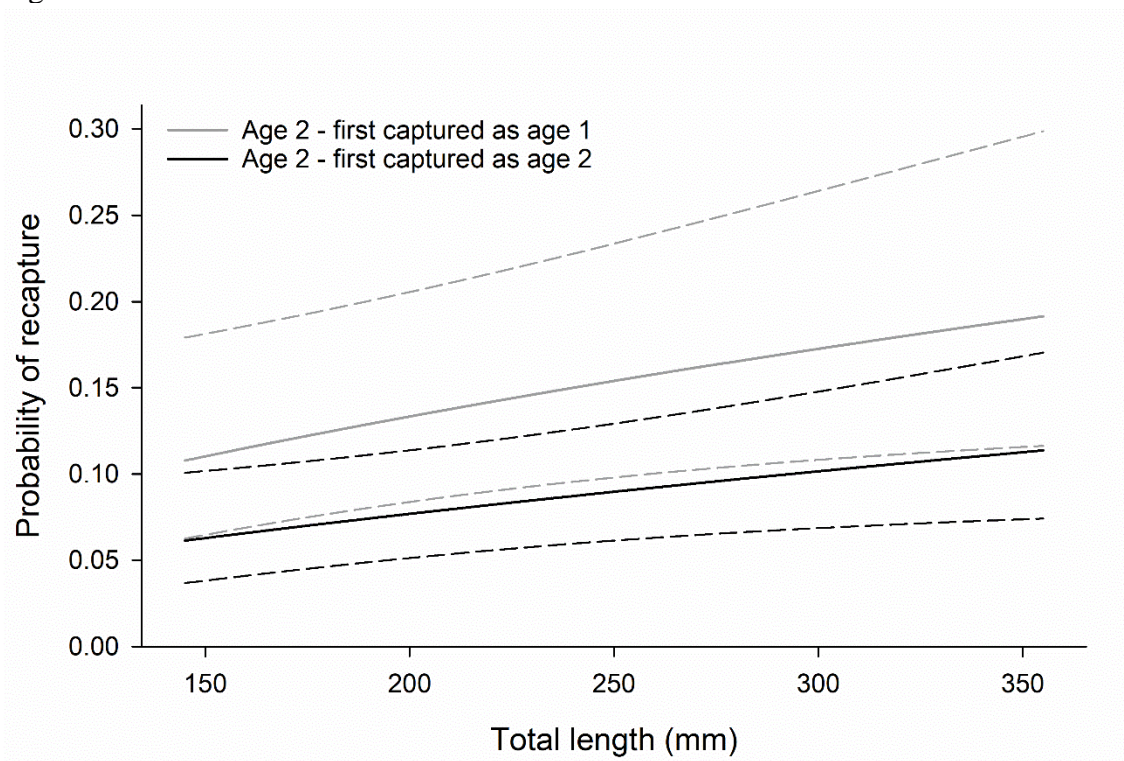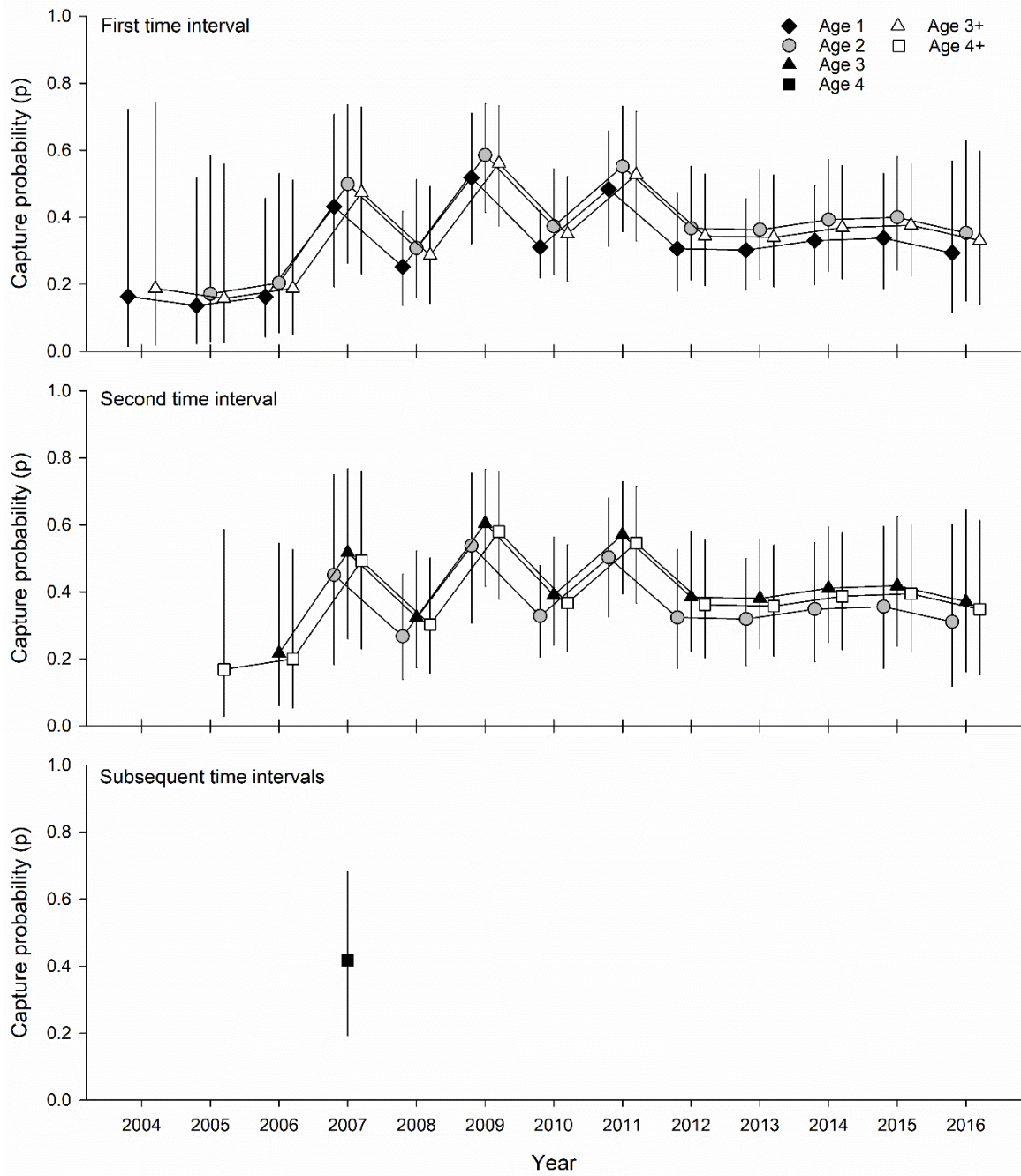

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720   Fig. 6.

721

722   Fig. 7.

723

724   Fig. 8.

Table S1. Representation of the ϕ time structure (*C1t+C2t+t*) receiving the highest support in the final

model set. Numbers correspond to unique survival and capture probability estimates across sampled

years. The first diagonal (dark grey) represents the first time interval (capture effect *C1t*; allowing for

annual variability), the second diagonal (white) represents the second time interval (capture effect *C2t*),

and the remaining cells (light grey) correspond to the 'time' (*t*) component of the model structure. These

estimates correspond to the apparent survival and capture probability estimates presented in figures 5 and

8 (panels match matrix diagonals). A total of six matrices (ϕ and p for all three age-groups) were

evaluated in each model.

	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
2003	1	14	26	27	28	29	30	31	32	33	34	35	36
2004		2	15	27	28	29	30	31	32	33	34	35	36
2005			3	16	28	29	30	31	32	33	34	35	36
2006				4	17	29	30	31	32	33	34	35	36
2007					5	18	30	31	32	33	34	35	36
2008						6	19	31	32	33	34	35	36
2009							7	20	32	33	34	35	36
2010								8	21	33	34	35	36
2011									9	22	34	35	36
2012										10	23	35	36
2013											11	24	36
2014												12	25
2015													13

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