Use of Ultrasonic Telemetry to Estimate Natural and Fishing Mortality of Red Snapper
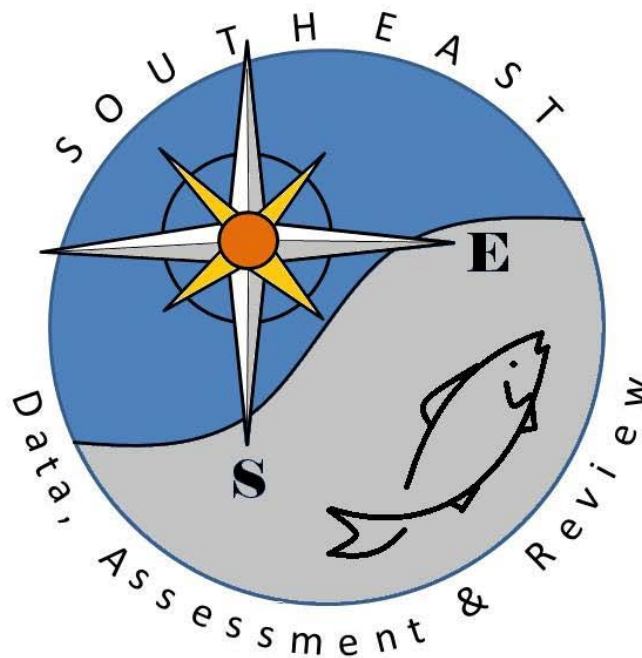
Topping and Szedlmayer

SEDAR31-DW13

6 August 2012

Please cite as:

Topping, D. and S.T. Szedlmayer. 2012. Use of Ultrasonic Telemetry to Estimate Natural and Fishing Mortality of Red Snapper . SEDAR31-DW13. SEDAR, North Charleston, SC. 45 pp.

1 **Draft in review, please do not cite without permission of authors**

2

3 **Use of Ultrasonic Telemetry to Estimate Natural and Fishing Mortality of**

4 **Red Snapper**

5

6

7 Darin T. Topping*[1] and Stephen T. Szedlmayer

8 *Department of Fisheries and Allied Aquacultures, Auburn University, 8300 State Hwy 104,*

9 *Fairhope, AL 36532, USA*

10

11

12

13 Running head: Natural and Fishing Mortality of Red Snapper

14

15

16

17 *Corresponding author: Darin T. Topping, darin.topping@myfwc.com, phone: 562 858-5332,

18 Fax: 352 543-6958

19 [1]Present address: Senator George G. Kirkpatrick Marine Laboratory, Fish and Wildlife Research

20 Institute, 11350 SW 153rd Court, Cedar Key, Florida 32625, USA

21

22

23 *Abstract*

24   An accurate estimate of natural mortality (M) is critical for the management of any fishery,

25 but is typically difficult to directly measure. Mortality rates for red snapper *Lutjanus*

26 *campechanus* ($N = 87$) were estimated from telemetry from December 2005 to June 2009 in the

27 northeastern Gulf of Mexico. At five separate sites an array of five receivers was deployed with

28 one receiver at the center (reef) and four receivers placed 1100 m (or 420 m) north, south, east,

29 and west of center. These arrays enabled the direct estimation of fishing mortality (F), natural

30 mortality (M), and emigration of acoustically tagged red snapper. Out of the 70 fish that

31 remained at the site for the 6-d recovery period, 19 were caught, 10 died naturally, and 28

32 emigrated from the 2-km radius study sites. The Kaplan-Meier (K-M) and staggered entry K-M

33 methods were used to estimate survival from different mortality events, and survival was

34 converted to instantaneous mortality rates. Ricker methods were also used to estimate mortality

35 rates. Overall all years combined total mortality (Z) ranged from 0.43 to 0.50, F from 0.30 to

36 0.38, and M from 0.12 to 0.22. More importantly, M estimated for each year changed from 0 in

37 2006, to 0.23-0.28 in 2007 and 0.17-0.20 in 2008, while annual F rates declined from 0.62-0.80

38 in 2006 to 0.24-0.25 in 2007 and 0.14 – 0.17 in 2008. Thus, in more recent years (2007-2008) M

39 may have increased, while F may have decreased compared to past estimates ($M = 0.1$; $F = 0.35$)

40 used in stock assessments. These higher levels of M coupled with the decreasing rates of F over

41 2006 to 2008 suggests that in recent years restrictive management efforts may have

42 accomplished the goal of reaching $F_{SPR26\%}$.

43

44

INTRODUCTION

45

46   Historically, red snapper *Lutjanus campechanus* have supported important commercial and

47   recreational fisheries in the Gulf of Mexico and are found over both natural and artificial reef

48   habitats (Camber 1955; Moseley 1966; Beaumariage 1969; Bradley and Bryan 1975; Fable 1980;

49   Stanley and Wilson 1989; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998;

50   Patterson et al. 2001; Szedlmayer and Schroepfer 2005; Westmeyer et al. 2007). Although

51   approximately 14,000 of these artificial habitats have been built in the northern Gulf of Mexico,

52   possibly enhancing available habitat for this reef oriented species (Minton and Heath 1998;

53   Gallaway et al. 2009), a recent assessment showed that the red snapper fishery was overfished

54   (SEDAR 2009). To rebuild red snapper stocks, managers set an objective of rebuilding stock

55   biomass to a maximum sustainable yield (MSY = 25.4 million pounds) by 2032, which may be

56   accomplished with an instantaneous fishing mortality rate (F) of Fmsy = $F_{\text{SPR 26\%}}$ (F at 26 %

57   spawning potential ratio; SEDAR7 2005; DEIS 2006; SEDAR 2009). This objective was based

58   on a conservative assumption of instantaneous natural mortality (M) equal to 0.10/year; however,

59   if M was actually higher, the goal of MSY may be achieved in a shorter period of time

60   (Goodyear 1995; Schirripa and Legault 1999; Slipke and Maceina 2005). Therefore, to allow for

61   an appropriate fishing level for red snapper in the northern Gulf of Mexico, it is important to

62   obtain an accurate estimate of M.

63   The red snapper fishery has continued for well over a century, and like most exploited fish

64   stocks, the level of M for red snapper in the Gulf is not well defined (Camber 1955; Schirripa

65   and Legault 1999). Total mortality (Z) has been obtained for red snapper from fishery

66   independent catch curve analysis (Gitschlag et al. 2003; Szedlmayer 2007); however, the

67   separation of Z into its components of M and F has been difficult. Estimates of M for red snapper

68   have been primarily derived from life history parameter equations based on maximum age, Von

69   Bertalanffy growth coefficient K, and water temperature, with estimates of M for red snapper

70   ranging from 0.02 to 0.40, with 95% confidence intervals from 0.02 to 1.0 (Alverson and Carney

71   1975; Pauly 1980; Nelson and Manooch 1982; Hoenig 1983; Goodyear 1995; Schirripa and

72   Legault 1999). The presently applied value of M (0.10) is based on maximum ages of red

73   snapper around 40 to 50 years (Hoenig 1983; Szedlmayer and Shipp 1994; Schirripa and Legault

74   1999; Wilson and Nieland 2001; SEDAR7 2005). This value of M (0.10) is conservative when

75   compared to estimates of M based on other life history parameters. This uncertainty in M has

76   lead to cautious management practices and severe reductions in fishery quotas (Hood et al.

77   2007). Despite its critical importance in population assessment, direct estimates natural mortality

78   for red snapper have not been reported in the literature.

79   Recent advances in telemetry systems, such as continuous automated monitoring, long-life

80   transmitters, and long distance detection, have allowed researchers to directly estimate natural

81   and fishing mortality in both fresh and saltwater environments (Hightower et al. 2001; Heupel

82   and Simpfendorfer 2002; Pine et al. 2003; Pollock et al. 2004; Young and Isely 2004; Starr et al.

83   2005). With these advances in technology, estimates of mortality are possible for species like red

84   snapper that inhabit large open water systems. In this study, strategic placement of remote

85   telemetry receivers allowed separation of total declines in tagged fish into its component parts of

86   emigration, natural mortality, and fishing mortality.

87

88   **METHODS**

Study Area

89

90   The study sites were located 20 to 30 km south of Mobile Bay, Alabama, USA, an area that

91   includes numerous artificial habitats (> 10,000) and a few natural rock-reef habitats (Schroeder

92   et al. 1988; Minton and Heath 1998). Red snapper were tagged on one natural and four artificial

93   habitats. Artificial habitats included a pipeline covered with a concrete mat (A1), a 15-m sunken

94   barge (A2), a 4.4 x 1.3 x 1.2 m steel metal cage (A3), and an M-60 army tank (A4). The natural

95   habitat site (N1) was composed of a 20-m long drowned river bed (~1 m high, ~5 m apart), with

96   undercut banks lined with tree stumps (Figure 1). Depths of the sites ranged from 20–30 m.

97   These sites were a mix of public (published latitude longitude) and private locations (Figure 1).

98

Fish Tagging

99

100   Red snapper (> 500 mm total length [TL]) were captured at the sites via hook and line, and

101   tagged with ultrasonic transmitters (Szedlmayer and Schroepfer 2005). Fish were placed in a 70-

102   L container of seawater containing MS-222 (150 mg MS-222/L seawater), and quickly

103   anesthetized (level 4; Summerfelt & Smith 1990). Fish were weighed and measured, and an

104   ultrasonic transmitter was implanted through a small (18 mm) vertical incision into the peritoneal

105   cavity with a No. 11 scalpel slightly above the ventral midline, and then sutured with plain gut

106   suture (Ethicon, no. 2, 3.5 metric). An internal anchor tag (Floy) was also inserted into the

107   incision before it was sutured. Sterile surgical methods and betadine were used throughout the

108   procedure. The fish were released after being held at the surface for a short (~1 min) recovery

109   period (when strong fin and gill movements were observed). Fish were released at the capture

110   site by lowering fish to the bottom with weighted line with an inverted barbless hook that was

111 attached to the fish's lower jaw. Retrieval of the weighted line released the fish at the bottom

112 near the reef.

113 Two types of transmitters were used for this study. Individually coded Vemco transmitters

114 (V16-6L-R64K; code intervals: 20 to 69 s, 16 x 94 mm, battery life: 6 years) were used at sites

115 with Vemco VR2 receivers, and Sonotronics transmitters (CT-05-48; continuous, 16 x 79 mm,

116 battery life: 4 years) were used at site A4 with Sonotronics SUR-1 receivers. Maximum detection

117 ranges were 1600 m for Vemco and 600 m for Sonotronics transmitters. The effects of

118 transmitter implantation on behavior or health of red snapper were assumed to be negligible after

119 a 6 d recovery period, because transmitter weights were < 2% of the total body weight of the fish

120 (Winter 1983; Adams et al. 1998; Brown et al. 1999).

121

122 **Continuous Remote Monitoring**

123 An underwater acoustic receiver array was deployed at each site that included five separate

124 omni-directional receivers (Vemco VR2 or Sonotronics SUR) moored ~5 m above the bottom.

125 For each array, one receiver was located at the release site [Center (C)] and the other four were

126 placed at 1100 m (VR2) or 420 m (SUR) to the North (N), South (S), East (E), and West (W) of

127 the center (Figure 2). Receivers placed at 1100 m (or 420 m) away from the center receiver were

128 predicted to result in complete detection of the fish within a ~2 km (VR2) or 1-km (SUR) radius

129 of the release sites (Szedlmayer and Schroepfer 2005). Receivers were coated with copper based

130 antifouling paint to prevent possible signal occlusion due to biofouling (Heupel et al. 2008).

131 Detection patterns of fish by these arrays identified if a fish was caught (fishing mortality),

132 died (natural mortality), or emigrated. Fishing mortality was also estimated from tag returns by

133   fishers. For example, a fishing mortality was identified by a detection pattern that would show

134   consistent, continuous detections at the center site, followed by a sudden loss of detections at

135   time of capture. Emigration was shown as a decrease in detections of a fish at the center site

136   followed by an increase in detections at a surrounding receiver prior to complete detection loss.

137   A natural mortality was identified when a fish stopped being detected at any outside receiver but

138   was still detected by the center receiver. This natural mortality detection pattern resulted from a

139   lack of fish movement and decrease in detection range from a transmitter that was lying on the

140   bottom. Each site was periodically surveyed with SCUBA divers, aided with a hand-held

141   receiver, to visually identify live fish with external tags and transmitters, and search for

142   stationary transmitters laying on the substrate from fish mortalities. A stationary control

143   transmitter was placed 400 m (VR2) or 150 m (SUR) south of the center location at each site to

144   estimate changes in detection range throughout the study, and enabled contrasts between

145   movements and mortality (Topping and Szedlmayer 2011a).

146

147   **Estimates of Mortality**

148   Several methods were used to calculate mortality rates, including equations defined by Ricker

149   (1975), Kaplan and Meier (1958), and Pollock et al. (1989).

150   *Ricker method*.–Annual exploitation rates (u) were derived from tag returns and telemetry-

151   identified fishing mortalities. Exploitation rates were calculated each month as the number of

152   tagged fish captured that month out of the number of tagged fish at risk of being captured at the

153   start of that month. The number of fish at risk at the start of each month was calculated as the

154   fish present at the start of the previous month minus all mortalities (fishing and natural) plus new

155   fish released during the previous month. An adjustment was made to the number of fish at risk

156   that accounted for non-reporting and natural mortalities of fish that emigrated from the sites. The

157   adjustment was based on the rates (proportion) of fisher non-reporting and natural mortality

158   estimated for fish that remained at the sites, and assumes that fish emigrating will incur the same

159   mortality rates as fish remaining within the receiver detection range at a site. A mean yearly rate

160   was calculated by multiplying the mean monthly u by 12. Expectation of natural death (v) was

161   calculated monthly from telemetry-detected natural mortalities at each site, and is defined as the

162   number of tagged fish dying naturally that month out of the number of tagged fish at risk of

163   dying at the start of that month. The number of fish at risk of dying at the start of each month

164   was calculated as the fish present at the start of the previous month minus all mortalities (fishing

165   and natural) plus new fish released during the previous month. Also, all fish that emigrated the

166   previous month were removed from the fish at risk so that natural death rate was only calculated

167   for fish remaining at the site, because natural mortality could not be detected for fish that

168   emigrated. To estimate annual rates of instantaneous fishing mortality (F) and natural mortality

169   (M), two estimates of instantaneous total mortality (Z) were applied. Total mortality (Z) was

170   estimated from the present telemetry derived estimates of u and v, and from catch-curve analysis

171   in previous studies ($Z = 0.54$; Gitschlag et al. 2003; Szedlmayer 2007). Annual survival (S) was

172   either calculated from the catch-curve or from u and v.

173   Three separate models were used to estimate M and F (Ricker 1975). Ricker model (1),

174   where $F = u\,Z\,/\,(1 - S)$ was used to calculate F from the telemetry-based u and the catch curve

175   derived $Z = 0.54$ (with $S = e^{-Z}$), then M was estimated by subtraction ($M = Z - F$). Ricker model

176   (2), where $M = v\,Z\,/\,(1 - S)$ was used to calculate M from the telemetry-based v and the catch

177   curve derived $Z = 0.54$ (with $S = e^{-Z}$), then F was estimated by subtraction ($F = Z - M$). In Ricker

178   model (3), both M and F were calculated separately from telemetry-based estimates of u, v, and

179   Z, using Ricker models (1) and (2), with $S = 1 - (u + v)$ and $Z = \log_e(S)$.

180

181   *Kaplan-Meier method.*–Mortality rates were calculated from the survival function, $S(t)$,

182   estimated from the product limit method of Kaplan and Meier (1958), which gives the

183   probabilities (S) of surviving a specified event (i.e. fishing, natural, or total mortality) over a

184   given time (t). This method allows for removal (right-censor) of fish that were not subject to the

185   particular mortality under analysis. For example, when estimating survival from natural mortality

186   events, fish caught and fish that emigrate from the site are censored from the analysis at the point

187   of that event occurring (i.e. fish did not experience a natural mortality up to the time of the

188   emigration or capture and are no longer at risk of a natural mortality). The Kaplan-Meier (K-M)

189   event analysis method was applied using the survival function:

190     $$\hat{S}(t) = \Pi_{tj \leq t}\, (1 - d_j / r_j);$$

191   the probability of surviving to t, where t is the time over which survival is estimated from the

192   product of the conditional probabilities of survival at each event point j, and where d_j represents

193   the number of individuals experiencing an event and r_j represents the number of individuals at

194   risk of an event at time t_j (Kaplan and Meier 1958; Allison 1995; Schroepfer and Szedlmayer

195   2006).

196   The SAS Lifetest procedure was used to estimate the survival to t assuming fish are released

197   on the same day and examines the entire distribution of event and censor times (Allison 1995).

198   Survival was then estimated at 365 days. By analyzing event times with respect to the same start

199 date, the effects of low sample size (in the beginning of the study) on K-M survival estimates are

200 removed. Survival functions were estimated separately for *M*, *F*, and *Z*. For example, for survival

201 from fishing mortality (event), fish that emigrated and died naturally were right censored from

202 the fish at risk. In this method, individuals censored are assumed to have the same prospect of

203 survival as individuals remaining at the study site. Since survival estimates are independently

204 derived by only considering the specified mortality event, instantaneous annual mortality rates

205 were calculated using the following equations:

206
$$F = - \log_e[S_F(365)],$$

207 where survival is based on probability of surviving fishing mortality over a year;

208
$$M = - \log_e[S_M(365)],$$

209 where survival is based on probability of surviving natural mortality over a year;

210
$$Z = - \log_e[S_Z(365)],$$

211 where survival is based on probability of surviving any mortality over a year. Variances for K-M

212 survival estimates were defined by Cox and Oakes (1984) as

213
$$\mathrm{Var}[\hat{S}(t)] = [\hat{S}(t)]^2 \, [1 - \hat{S}(t)] \, / \, r(t),$$

214 and 95% confidence intervals for K-M were defined by Pollock et al. (1989) as

215
$$\hat{S}(t) \pm 1.96[\mathrm{var} \ \hat{S}(t)]^{\frac{1}{2}}.$$

216 Ranges of mortality rates were calculated from the 95% confidence interval ranges of the

217 survival functions at a time of 365 d.

218

219 *Staggered entry method.*–The staggered entry method is a modification of the previous K-M

220 survival function method and has been applied to telemetry data (Pollock et al. 1989; Heupel and

221   Simpfendorfer 2002). The staggered entry equation is similar to the K-M, with the exception that

222   this method allows individuals to enter at any time during the study. Individuals that emigrated

223   or did not experience the specified mortality event over the given time period were right

224   censored as discussed above (e.g., a fish emigrating 200 d after release was known to survive a

225   mortality event for at least 200 d). In the staggered entry method, the number of fish at risk could

226   fluctuate from period to period depending on the number of fish present, new releases

227   (additions), and removals from the sites (fishing mortality, natural mortality, and emigrations) in

228   the previous period. The survival function was estimated by taking the product of the conditional

229   survival probabilities calculated every 30-d period up to the 1230-d study length (i.e. 42 time

230   periods). The mortality rate equations were adjusted to estimate an annual survival $S(365)$ from

231   the survival probabilities at the end of the study $S(1230)$ by applying an exponent of 365/1230

232   (e.g. F, M, or $Z = -\log_e[S(1230)^{365/1230}]$; Starr et al. 2005).

233

234   **RESULTS**

235   Red snapper ($N = 87$) were continuously monitored at five different sites (A1-A4, N1; Figure

236   1) for 1230 d (December 2005 to May 2009). Total length (TL) of tagged red snapper ranged

237   from 501 to 860 mm, with a mean of 639 mm (SD, 85 mm). These 87 fish remained present at

238   the site, emigrated, died, or were removed by fishers, as determined by detections from the five

239   receivers at each site and by fisher returns (e.g. Figure 3; Table 1). Event times (or minimum

240   residence time if still present) ranged from 0 to 1020 d (Table 1). Of the 87 tagged fish, 17 either

241   left the site or died within the first 6 d after release (14 emigrated, 2 died, and 1 unknown).

242   These events within the first 6 d post release were considered tagging artifacts, and no fish that

243   left within 6 d were detected again or returned by fishers. Thus, the 70 remaining fish were used

244   for mortality rate estimations, and data were analyzed up to 27 May 2009 (just prior to the 2009

245   fishing season).

246   There were 14 fish still present at the various sites at the end of the study (Table 1).

247   Additional emigrations were detected ($n = 27$) after the 6-d post-release period, with 2 fish in

248   2006, 9 fish in 2007, 14 fish in 2008, and 2 fish in 2009 leaving the site from 28 to 758 d after

249   release. Six fish from the 27 emigrations were last detected at a site when one of the five outer

250   array receivers was not functioning, but were assumed to have emigrated based on the detections

251   from other receivers at that site (unknowns [U]; Table 1). No natural mortalities were detected in

252   2006, but there were five in 2007, five in 2008, and none in 2009 (up to June 2009). There were

253   19 fishing mortalities at four sites (A1-A4, $F = 0$ at N1), with 17 fish returned by fishers and 2

254   estimated from telemetry detection data. Nine fish were caught in 2006, five in 2007, and five in

255   2008. Of the nine fish caught in 2006, all were caught at site A1 in April, May, and June, and six

256   were captured by one fisher. This fisher admittedly targeted this site. Overall, site A1 had the

257   highest fishing mortality (13 fish out of 20 released). Targeting of this study site may have

258   increased exploitation rates beyond actual levels in 2006 ($u = 0.50$, April; 0.75, June), as few fish

259   were at risk during the early part of this study (10 fish in April, 5 in May, and 6 in June). Both

260   the Ricker and staggered entry models are sensitive to low sample sizes in the beginning of the

261   study which resulted in negative or zero M values, and F values greater than 1.0. Because of the

262   fishing mortality bias from this particular fisher, these captures were censored in the Ricker and

263   right censored in the staggered entry analysis, and not included in the fishing mortality estimates

264   for these models, but the mortalities from this directed fisher were included K-M mortality

265   estimates.

266

Ricker Mortality Estimates

268   The mean yearly exploitation rate (u) was 0.25/year (SE, 0.12). The u decreased each year,

269   from 0.55/year (2006) to 0.19/year (2007) to 0.12/year (2008). The fisher capture reporting rate

270   was > 90% based on detections and tag returns, with only 2 fish out of 19 not returned by a

271   fisher. Natural death rate (v) over all sites was 0.11/year (SE, 0.04). No natural mortality was

272   detected in 2006, v was 0.22/year in 2007, and 0.17/year in 2008.

273   The Ricker model (1) mortality estimates were $F = 0.32$ and $M = 0.22$ (from subtraction),

274   based on a Z of 0.54 (Gitschlag et al. 2003; Szedlmayer 2007) and $u = 0.25$/year (Table 2). The

275   Ricker model (2) mortality estimates were $M = 0.14$ and $F = 0.40$ (from subtraction), based on

276   the same $Z = 0.54$ and $v = 0.11$/year (Table 2). Ricker model (3) mortality estimates were $F =$

277   0.30 and $M = 0.14$, based on estimates of $u = 0.25$/year, $v = 0.11$/year, and $Z = 0.44$ from the

278   present study (Table 2). Ricker model (3) was used to obtain mortality estimates by year from

279   above yearly estimates of u and v. In 2006, $F = 0.80$ and $M = 0.0$; in 2007, $F = 0.25$ and $M =$

280   0.28; and, in 2008, $F = 0.14$ and $M = 0.20$ (Table 3).

281

Kaplan-Meier Mortality Estimates

283   The estimation of mortality rates using the Kaplan-Meier (K-M) method were based on all

284   data ($n = 70$ fish). All fish were considered to be released on the same start date, and as such

285   there was not artificial inflation of mortality rates when few fish were at risk at the beginning of

286   the study. The overall rate of survival (S) from all mortality (fishing + natural) was 61% at 365 d

287   (S_Z[365]) or $Z = 0.50$ (Table 2; Figure 4). When survival from fishing mortality was estimated,

288     $S_F(365) = 68\%$ and $F = 0.38$ (Table 2; Figure 5). When survival from natural mortality was

289   estimated, $S_M(365) = 89\%$ and $M = 0.12$ (Table 2; Figure 5). If the K-M method was applied with

290   the recaptures from the fisher that targeted site A1 removed (right censored), $Z = 0.39$ and $F =$

291   0.27.

292   If the K-M method is applied to only 2007 and 2008 data ($n = 44$ fish), F would also decrease

293   from 0.45 to 0.31, but this would exclude most of the fish released at site A1. Site A1 had the

294   most fishing mortalities (13 of 20 fish), and was the first site established. If all sites except A1

295   were considered ($n = 50$ fish), F would be 0.20; however, if F was based only on site A1, F

296   would be 1.0. Site A4 had the second highest F (0.56), and was a public site. Site N1 was the last

297   site established (December 2007), and showed the lowest $F = 0$, compared to other sites.

298

299   **Staggered Entry Mortality Estimates**

300   The staggered entry method also showed sensitivity to low sample size in the beginning six

301   months of this study as shown in the Ricker method. After the first six months (June 2006), the

302   probability of survival (i.e., S_F[180]) dropped to 10% when all fishing mortalities were

303   considered, resulting in an F of 2.3, which is an unrealistic estimate. After removal of the

304   captures from the biased fisher, fishing mortality decreased, $S_F(365) = 74\%$ and $F = 0.31$ (Table

305   2; Figure 6). While no natural deaths were detected in 2006 (probably due to low sample size),

306   natural deaths were spread out relatively evenly in subsequent years. Survival from a natural

307   mortality using the K-M staggered entry was $S_M(365) = 89\%$, $M = 0.12$; and, survival from all

308   mortality was $S_Z(365) = 65\%$, $Z = 0.43$ (Table 2; Figure 7, 8). Mortality rate estimates based on

309   the staggered entry method varied by year (Table 3).

310

311   **DISCUSSION**

312   Ultrasonic telemetry allowed continuous, long-term (~ 3 years) monitoring of tagged red

313   snapper at the study sites. The arrangement of receivers enabled the estimation of emigration,

314   natural mortality, and fishing mortality at various habitat structures. An important advancement

315   in the present study was the use of stationary control transmitters at each site that allowed

316   monitoring detection range changes due to environmental factors throughout the study.

317   Knowledge of detection range and comparisons between detection patterns of stationary (dead

318   fish) and moving (live fish) transmitters were necessary for identifying emigration and mortality

319   events (Topping and Szedlmayer 2011a). Most studies that employed telemetry techniques to

320   estimate mortality of relatively mobile species (e.g., striped bass, blacktip sharks) have been

321   successful in semi-closed systems and generally have estimated natural mortalities based on lack

322   of movement (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Young and Isely 2004).

323   For example, Heupel and Simpfendorfer (2002) were able to directly detect fishing and natural

324   mortality of juvenile blacktip sharks in Terra Ceia bay by using a large number of VR2 receivers

325   to continuously monitor movement, lack of movement (mortality), sudden disappearance

326   (capture), and emigration of individuals from the mouth of the bay. More difficulty is

327   encountered when attempting to estimate mortality with telemetry in open ocean systems (vs

328   closed), and has been limited to fish that show moderate residence (Starr et al. 2005). In the

329   present study, high site fidelity of red snapper to reef sites (Szedlmayer and schroepfer 2005;

330 Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a, b) provided an opportunity to

331 directly estimate mortality rates and emigration of red snapper for the first time in a large open

332 water system (i.e., northern continental shelf of the Gulf of Mexico).

333 Values of F for some stock assessments are dependent on M, in which M is determined

334 indirectly from the life history parameter equations, with F only as accurate as M (Manooch et al.

335 1998). Estimates of M derived indirectly from life history parameters for red snapper from the

336 northern Gulf of Mexico (Table 4; e.g. maximum age, maximum weight, K, water temperature)

337 can range from 0.08 to 0.36 (Chen and Watanabe 1989; Pauly 1980; Hoenig 1983; Peterson and

338 Wroblewski 1984; Jensen 1996; Quinn and Deriso 1999; Slipke and Maceina 2005; Wilson and

339 Nieland 2001; Szedlmayer 2007). The most recent red snapper fishery assessment used a

340 conservative M of 0.10, which was lowered from the 0.20 used in an earlier assessment

341 (Goodyear 1995; Schirripa and Legault 1999; SEDAR7 2005; SEDAR 2009). The predicted M

342 was lowered due to evidence of older fish (up to 53 years) in the stock (Szedlmayer and Shipp

343 1994; Schirripa and Legault 1999; Wilson and Nieland 2001). Over all years combined the direct

344 estimates of M from telemetry methods in this study (0.12–0.22; 95% CL = 0.04–0.27; Table 2)

345 were consistent with estimates from the indirect methods (0.08–0.36; Table 4), but higher than

346 the estimate of M used in the most recent assessment (0.10). The present study provides the only

347 empirically derived estimates of M for red snapper, however such estimates will probably change

348 from year to year depending on environmental conditions or from possible increases in density-

349 dependent mortality associated with population increase during the red snapper stock rebuilding

350 phase (Rose et al. 2001; Gazey et al. 2008).

351   Detection of changes in natural mortality rates among years or shorter periods of time

352   (Young and Isely 2004) or during catastrophic environmental conditions (e.g. hurricanes or dead

353   zones) could be efficiently assessed with the present telemetry methods. There were no natural

354   deaths detected in 2006 probably due to the combination of low sample size and the high number

355   of released fish caught by fishers early in the study. In the following years, M was higher based

356   on the staggered entry method (0.23 in 2007; 0.17 in 2008). The Ricker model-3 also showed

357   higher estimates of in 2007 ($M = 0.28$) and 2008 (0.20) than 2006 (0). We suggest that these later

358   estimates of M (0.17 to 0.28) are probably better estimates of actual red snapper natural mortality

359   rates, because of greater sample size and reduced fishing mortality.

360   Over all years combined the direct estimates of F in this study (0.30–0.40; 95% CL 0.24–

361   0.64) were similar to $F = 0.35$ for red snapper from the 2005 stock assessment (SEDAR7 2005)

362   and $F = 0.29$ to 0.47 from the 1999 stock assessment (Schirripa and Legault 1999). However, F

363   showed substantial annual variation during this study. The higher exploitation rates in 2006 for

364   the present study may be lower sample sizes inflating exploitation, but also may reflect changes

365   in fishing regulations among years. Total allowable catch (TAC) quotas were decreased from 9.1

366   million pounds (MP) in 2006, to 6.5 MP in 2007, and to 5.0 MP in 2008. These reductions in

367   TAC resulted in more restrictive seasonal and bag limits. For example, in 2006 the federal waters

368   were open to recreational red snapper fishing for seven months (April to October 2006) with a

369   four fish bag limit (407 mm TL minimum size), in 2007 a two fish bag limit was instituted, and

370   in 2008 the fishing season was limited to two months (June and July 2008). Though it is difficult

371   to compare the first year of the study due to low sample size, the decreasing pattern of fishing

372   mortality from 2006 to 2008 in the present telemetry study appeared to reflect the changes in

373 fishery management regulations. Fishing mortality (F) was 0.80 in 2006, 0.25 in 2007, and 0.14

374 in 2008 (Ricker model 3).

375 Detection of a fishing mortality event based on telemetry detection data was validated by

376 fisher returns ($n = 17$ fisher returns out of 19 telemetry detected fishing mortalities). Confidence

377 in the accuracy of detection of M was $< F$ since we were not able to retrieve all of the

378 transmitters from dead fish. However, even when independently estimating each type of

379 mortality event, there was a convergence of mortality rates estimated among the various methods

380 (low variability), which increases confidence in the accuracy of M. Total mortality (Z) estimates

381 showed low variance among the methods used, with estimates of 0.50 (K-M), 0.43 (staggered

382 entry), and 0.44 (Ricker model 3), which are similar to a Z of 0.54 obtained by both Gitschlag et

383 al. (2003) and Szedlmayer (2007) from catch curves of completely separate fishery independent

384 surveys. Although the different methods of estimating mortality showed similar results, there

385 were advantages and disadvantages of each method. The staggered entry (modified K-M;

386 Pollock et al. 1989) and K-M methods simplify calculations, with only data needed on the time

387 from release till an event, an emigration, or if a fish is still present. The staggered entry method

388 is suggested as the preferred method if there is a reasonably high initial release of individuals

389 into the study, and this method allows for additional individuals to be added throughout the study

390 (Heupel and Simpfendorfer 2002). Also, this would be the best method to show seasonal or

391 yearly fluctuations in survival if there are similar sample sizes among periods. The confidence

392 intervals used for the staggered entry method narrowed as the study progressed because sample

393 size increased as more fish were released over the study. The K-M method was the least sensitive

394 to fluctuations in sample size and periods of high mortality. The K-M method showed narrower

395   95% confidence limits in the beginning of the study due to the "release" of all fish ($n = 70$) at

396   day 0. Accuracy of this method is affected by the length of the study, with confidence increasing

397   as more fish progress through the study to experience an event.

398   The traditional Ricker (1975) methods using u or v rates and some estimate of Z to calculate

399   F or M, were similar to the staggered entry method. The same time periods (30 d) were used to

400   estimate u and v (Ricker), and survival (staggered) with similar numbers of fish at risk at the

401   beginning of each period. Since the estimates of F may have been more accurate (than M) due to

402   validation of detection data with fisher returns, Ricker model 1 ($u = 0.25$/year, $Z = 0.54$) may

403   give the most accurate estimate of M (0.22). Again, the major disadvantage with the Ricker

404   method is overestimating exploitation rates when few fish are at risk, as in the beginning of this

405   study.

406   Since M represents a measure of the longevity and natural rate of replacement of the

407   population, higher values of M may allow for higher catches in the fishery; however, if the

408   fishery is managed assuming a high M when its value is much lower, there may be significant

409   problems (Schirripa and Legualt 1999; Slipke and Maceina 2005). Over all years combined the

410   natural mortality rates estimated in this study (0.12–0.22) were slightly above to more than

411   double the $M = 0.10$ used in past red snapper fishery assessments. More importantly, M

412   estimated for each year changed from 0 in 2006, to 0.23-0.28 in 2007 and 0.17-0.20 in 2008.

413   Thus, the present study suggest that natural mortality is higher than past estimates, and may have

414   actually increased to as much as three times the past rates used in stock assessments during the

415   red snapper rebuilding period under restrictive management. This higher level of M coupled with

416   the decreasing rates of F in 2007 (0.24-0.25) and 2008 (0.14-0.17) suggests that the goal of

417 $F_{SPR26\%}$ may have been reached in recent years and further reductions of fishing quotas may be

418 unnecessary.

419

420

421 **REFERENCES**

422 Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998. Effects of surgically and

423 gastrically implanted radio transmitters on growth and feeding behavior of juvenile chinook

424 salmon. Transactions of the American Fisheries Society. 127:128–136.

425 Allison, P. D. 1995. Survival analysis using the SAS® System: a practical guide. SAS Institute,

426 Cary, North Carolina.

427 Alverson, D. L., M. J. Carney. 1975. A graphic review of the growth and decay of population

428 cohorts. Journal du Conseil International pour l'Exploration de la Mer 36:133–143.

429 Beaumariage, D.S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative

430 analysis of previous results. Florida Department of Natural Resources Technical Series 59:1–

431 38.

432 Bradley, E., and C. E. Bryan. 1975. Life history and fishery of the red snapper (*Lutjanus*

433 *campechanus*) in the Northwestern Gulf of Mexico. Gulf and Caribbean Fisheries Institute

434 27:77–106.

435 Brown, R. S., J. C. Steven, W. G. Anderson, and R. S. McKinley. 1999. Evidence to Challenge

436 the ''2% Rule'' for Biotelemetry. North American Journal of Fisheries Management 19:867–

437 871.

438   Camber, C. I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special

439   reference to the Campeche Banks. Florida Board of Conservation Technical Series 12:1–64.

440   Chen, S., and S. Watanabe. 1989. Age dependence and natural mortality coefficient in fish

441   population dynamics. Nippon Suisan Gakkaishi 55:205–208.

442   Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman and Hall, New York.

443   DEIS. 2006. Draft environmental impact statement to evaluate alternatives to set Gulf of Mexico

444   red snapper total allowable catch and reduce bycatch in the Gulf of Mexico directed and

445   shrimp trawl fisheries. NOAA, NMFS, St. Petersburg, Florida USA.

446   Fable Jr, W. A. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion

447   snapper (*Rhomboplites aurorubens*) off the South Texas coast. Contributions in Marine

448   Science 23:115–121.

449   Gallaway, B. J., S. T. Szedlmayer, and W. J. Gazey. 2009. A life history review for red snapper

450   in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms

451   and other artificial reefs. Reviews in Fisheries Science 17:48–67.

452   Gazey, W. J., B. J. Gallaway, J. G. Cole, and D. A. Fournier. 2008. Age composition, growth,

453   and density–dependent mortality in juvenile red snapper estimated from observer data from

454   the Gulf of Mexico penaeid shrimp fishery. North American Journal of Fisheries

455   Management 28:1828–1842.

456   Gitschlag, G. R., M. J. Schirripa, and J. E. Powers. 2003. Impacts of red snapper mortality

457   associated with the explosive removal of oil and gas structures on stock assessments of red

458   snapper in the Gulf of Mexico. *In* Fisheries, reefs, and offshore development, Stanley, D. R.,

459   and A. Scarborough-Bull, Editors. American Fisheries Society, Symposium 36:83–94.

460   Goodyear, C. P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. NMFS-SEFSC

461   Contribution: MIA-94/94-63. Miami, Florida.

462   Heupel, M. R., and C. A. Simpfendorfer. 2002. Estimation of mortality of juvenile blacktip

463   sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal

464   of Fisheries and Aquatic Sciences 59:624–632.

465   Heupel, M. R., K. L. Reiss, B. G. Yeiser, and C. A. Simpfendorfer. 2008. Effects of biofouling

466   on performance of moored data logging acoustic receivers. Limnology and Oceanography:

467   Methods 6:327–335.

468   Hightower, J. E., J. R. Jackson, K. H. Pollock. 2001. Use of telemetry methods to estimate

469   natural and fishing mortality of striped bass in Lake Gaston, North Carolina. Transactions of

470   the American Fisheries Society 130:557–567.

471   Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin

472   82:898–903.

473   Hood, P. B., A. J. Strelcheck, and P. Steele. 2007. A history of red snapper management in the

474   Gulf of Mexico. Pages 267–284 *in* W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and

475   D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico.

476   American Fisheries Society Symposium, 60, Bethesda, Maryland.

477   Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of

478   reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53:820–822.

479   Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations.

480   Journal of the American Statistical Association 53:457–481.

481   Manooch III, C. S., J. C. Potts, D. S. Vaughan, and M. L. Burton. 1998. Population assessment

482   of the red snapper from the southeastern United States. Fisheries Research 38:19–32.

483   Minton, R. V., and S. R. Heath. 1998. Alabama's artificial reef program: building an oases in the

484   desert. Gulf of Mexico Science 16:105–106.

485   Moseley, F. N. 1966. Biology of the red snapper, *Lutjanus aya* Block, of the northwestern Gulf

486   of Mexico. Publications of the Institute of Marine Science University of Texas 11:90–101.

487   Nelson, R. S., and C. S. Manooch III. 1982. Growth and mortality of the red snapper, *Lutjanus*

488   *campechanus*, in the west-central Atlantic and northern Gulf of Mexico. Transactions of the

489   American Fisheries Society 111:465–475.

490   Patterson III, W. F., J. C. Watterson, R. L. Shipp, and J. H. Cowan Jr. 2001. Movement of tagged

491   red snapper in the Northern Gulf of Mexico. Transactions of the American Fisheries Society

492   130:533–545.

493   Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters, and mean

494   environmental temperature in 175 fish stocks. Journal du Conseil International pour

495   l'Exploration de la Mer 39:175–192.

496   Peabody, M. B. 2004. The fidelity of red snapper (*Lutjanus campechanus*) to petroleum

497   platforms and artificial reefs in the northern Gulf Of Mexico. Master's Thesis. Louisiana

498   State University, Baton Rouge, Louisiana.

499   Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem.

500   Canadian Journal of Fisheries and Aquatic Sciences 41:1117–1120.

501 Pine, W. E., K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of

502   tagging methods for estimating fish population size and components of mortality. Fisheries

503   28:10–23.

504 Pollock, K. H., H. Jiang, and J. E. Hightower. 2004. Combining telemetry and fisheries tagging

505   models to estimate fishing and natural mortality rates. Transactions of the American

506   Fisheries Society 133:639–648.

507 Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in

508   telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

509 Quinn II, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press,

510   New York.

511 Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations.

512   Fisheries Research Board of Canada Bulletin 191.

513 Rose, K. A., J. H. Cowan Jr, K. O. Winemiller, R. A. Myers, and R. Hillborn. 2001.

514   Compensatory density dependence in fish populations: importance, controversy,

515   understanding and prognosis. Fish and Fisheries 2:293–327.

516 Schroeder, W. W.,A. W. Shultz, and J. J. Dindo. 1988. Inner-shelf hardbottom areas,

517   northeastern Gulf of Mexico. Gulf Coast Association of Geological Societies Transactions

518   38: 535–541.

519 Schroepfer, R. L., and S. T. Szedlmayer. 2006. Estimates of residence and site fidelity for red

520   snapper *Lutjanus campechanus* on artificial reefs in the northeastern Gulf of Mexico.

521   Bulletin of Marine Science 78:93–101.

522   Schirripa, M. J., and C. M. Legault. 1999. Status of the red snapper in U.S. waters of the Gulf of

523   Mexico: updated through 1998. Southeast Fisheries Science Center, Miami Laboratory,

524   NMFS, SFD-99/00-75.

525   SEDAR7. 2005. Stock assessment report of SEDAR 7, Gulf of Mexico Red Snapper. NMFS,

526   SEFSC, NOAA, Charleston, South Carolina. Available: http://www.sefsc.noaa.gov.(January

527   2009).

528   SEDAR. 2009. Stock Assessment of Red Snapper in the Gulf of Mexico: SEDAR Update

529   Assessment. NMFS, SEFSC, NOAA, Miami, Florida. Available:

530   http://www.sefsc.noaa.gov.(January 2009).

531   Slipke, J. W., and M. J. Maceina. 2005. Fisheries analyses and simulation tools (FAST 2.1).

532   Auburn University, Auburn, Alabama USA.

533   Stanley, D. R., and C. A. Wilson. 1989. Utilization of offshore platforms by recreational

534   fishermen and SCUBA divers off the Louisiana coast. Bulletin of Marine Science 44:767–

535   775.

536   Starr, R. M., V. O'Connell, S. Ralston, L. Breaker. 2005. Use of acoustic tags to estimate natural

537   mortality, spillover, and movements of lingcod (*Ophiodon elongatus*) in a Marine Reserve.

538   Marine Technology Society Journal 39:19–30.

539   Summerfelt, R. C., and L. S. Smith. 1990. Anesthesia, surgery, and related techniques. In:

540   Schreck, C. B., and P. B. Moyle (eds) Methods for Fishery Biology. Bethesda: American

541   Fisheries Society, 213–272.

542   Szedlmayer, S. T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial

543   reef sites in the northeast Gulf of Mexico. Copeia 1997:846–850.

544   Szedlmayer, S. T. 2007. An evaluation of the benefits of artificial habitats for red snapper,

545   *Lutjanus campechanus*, in the northeast Gulf of Mexico. Proceedings of the Gulf and

546   Caribbean Fisheries Institute 59:223-229.

547   Szedlmayer, S. T., and R. L. Schroepfer. 2005. Long-term residence of red snapper on artificial

548   reefs in the northeastern Gulf of Mexico. Transactions of the American Fisheries Society

549   134:315–325.

550   Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of red snapper, *Lutjanus*

551   *campechanus*, from an artificial reef area in the Northeastern Gulf of Mexico. Bulletin of

552   Marine Science 55:887–896.

553   Topping, D. T., and S. T. Szedlmayer. 2011a. Site fidelity, residence time and movements of red

554   snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring. Marine

555   Ecology Progress Series 437: 183–200.

556   Topping, D. T., and S. T. Szedlmayer. 2011b. Home range and movement patterns of red

557   snapper (*Lutjanus campechanus*) on artificial reefs. Fisheries Research

558   doi:10.1016/j.fishres.2011.08.013.

559   Watterson, J. C., W. F. Patterson III, R. L. Shipp, and J. H. Cowan Jr. 1998. Movement of red

560   snapper, *Lutjanus campechanus*, in the north central Gulf of Mexico: potential effects of

561   hurricanes. Gulf of Mexico Science 1998:92–104.

562   Westmeyer, M. P., C. A. Wilson, and D. L. Nieland. 2007. Fidelity of red snapper to petroleum

563   platforms in the northern Gulf of Mexico. Pages 105–121 *in* W. F. Patterson, III, J. H.

564   Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in

565   the U.S. Gulf of Mexico. American Fisheries Society Symposium, 60, Bethesda, Maryland.

566   Wilson, C. A., and D. L. Nieland. 2001. Age and growth of red snapper, *Lutjanus campechanus*,

567   from the northern Gulf of Mexico off Louisiana. Fishery Bulletin 99:653–664.

568   Winter, J. D. 1983. Underwater biotelemetry. Pages 371–395 In: L. A. Nielsen and D. L.

569   Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

570   Young, S. P., and J. J. Isely. 2004. Temporal and spatial estimates of adult striped bass mortality

571   from telemetry and transmitter return data. North American Journal of Fisheries Management

572   24:1112–1119.

573

574 Table 1. Summary of release information (total length, TL; weight, Wt) and number of days

575 (event time) from release until occurrence of the specified event (emigration = E, fishing

576 mortality = F, natural mortality = M, present = P, unknown = U) for ultrasonically-tagged red

577 snapper at various array sites.

Fish	Release	Site	Wt (kg)	TL (mm)	Event time (d)	Event
1	13-Dec-2005	A1	4.3	660	614	E
2	13-Dec-2005	A1	7.3	800	179	F
3	13-Dec-2005	A1	3.0	590	153	F
4	13-Dec-2005	A1	6.0	710	2	E
5	13-Dec-2005	A1	4.0	630	155	F
6	13-Dec-2005	A1	5.5	695	114	F
7	23-Dec-2005	A1	2.9	580	99	F
8	23-Dec-2005	A1	4.0	620	104	F
9	4-Jan-2006	A1	5.0	630	1	E
10	4-Jan-2006	A1	3.5	520	108	F
11	4-Jan-2006	A1	5.0	553	5	E
12	4-Jan-2006	A1	12.5	860	1	E
13	4-Jan-2006	A1	3.5	540	92	F
14	12-Jan-2006	A1	6.0	700	84	F
15	7-Jun-2006	A1	6.5	746	452	M

Fish	Release	Site	Wt (kg)	TL (mm)	Event time (d)	Event
16	7-Jun-2006	A1	2.8	545	324	F
17	8-Jun-2006	A1	4.7	672	1	E
18	15-Jun-2006	A1	4.5	683	321	M
19	23-Jun-2006	A4	3.3	586	733	E
20	7-Jul-2006	A4	3.2	600	420	E
21	11-Jul-2006	A1	3.7	620	741	F
22	11-Jul-2006	A1	8.2	815	1020	P
23	27-Jul-2006	A2	5.5	691	0	M
24	28-Jul-2006	A2	9.5	823	411	E
25	28-Jul-2006	A2	5.1	680	227	E
26	28-Jul-2006	A2	5.8	730	322	E
27	9-Aug-2006	A3	7.1	760	3	E
28	9-Aug-2006	A3	4.3	660	406	U
29	11-Aug-2006	A3	3.0	605	215	E
30	14-Aug-2006	A3	2.2	538	120	U
31	14-Aug-2006	A3	2.8	537	758	E
32	14-Aug-2006	A3	3.1	569	362	F
33	21-Aug-2006	A3	6.5	740	124	U
34	21-Aug-2006	A3	2.5	543	1	E

Fish	Release	Site	Wt (kg)	TL (mm)	Event time (d)	Event
35	7-Feb-2007	A2	3.3	555	530	M
36	7-Feb-2007	A2	5.8	690	572	U
37	7-Feb-2007	A3	2.6	549	4	E
38	7-Feb-2007	A3	3.8	610	28	E
39	7-Feb-2007	A3	4.5	640	534	M
40	7-Feb-2007	A3	3.5	580	1	E
41	7-Feb-2007	A3	4.0	613	57	M
42	6-Mar-2007	A1	5.0	665	6	E
43	6-Mar-2007	A1	4.8	660	46	F
44	3-Apr-2007	A2	5.5	690	144	E
45	3-Apr-2007	A2	5.3	680	1	E
46	12-Apr-2007	A3	2.8	565	479	M
47	12-Apr-2007	A3	2.8	555	122	F
48	12-Apr-2007	A3	4.5	670	776	P
49	21-May-2007	A2	2.5	550	210	M
50	21-May-2007	A2	11.0	800	750	P
51	12-Jun-2007	A3	2.5	590	711	P
52	27-Jun-2007	A1	6.5	645	542	E
53	3-Jul-2007	A2	5.0	705	30	M

Fish	Release	Site	Wt (kg)	TL (mm)	Event time (d)	Event
54	9-Jul-2007	A2	5.5	710	588	E
55	9-Jul-2007	A2	5.0	710	20	F
56	9-Jul-2007	A3	3.3	620	688	P
57	9-Jul-2007	A3	5.8	730	182	E
58	25-Jul-2007	A3	4.5	685	462	U
59	25-Jul-2007	A3	3.8	660	661	E
60	25-Jul-2007	A3	6.1	760	167	E
61	29-Aug-2007	A4	3.8	645	339	F
62	29-Aug-2007	A4	2.5	550	650	P
63	29-Aug-2007	A4	3.3	601	332	F
64	29-Aug-2007	A4	5.0	710	379	E
65	5-Sep-2007	A4	3.5	635	332	F
66	13-Nov-2007	A1	5.0	705	575	P
67	14-Nov-2007	A4	3.0	579	572	P
68	20-Nov-2007	A3	3.0	605	286	M
69	29-Nov-2007	A3	4.3	658	239	E
70	29-Nov-2007	A3	9.8	810	381	E
71	11-Dec-2007	N1	3.0	573	265	U
72	11-Dec-2007	N1	2.2	501	80	E

Fish	Release	Site	Wt (kg)	TL (mm)	Event time (d)	Event
73	11-Dec-2007	N1	2.5	550	6	E
74	11-Dec-2007	N1	1.9	517	547	P
75	18-Dec-2007	N1	2.6	557	1	U
76	18-Dec-2007	N1	2.2	524	4	E
77	8-Feb-2008	A1	3.6	640	47	M
78	8-Feb-2008	A1	3.3	615	121	F
79	10-Jun-2008	A2	3.8	640	336	P
80	10-Jun-2008	A2	7.8	790	364	P
81	10-Jun-2008	A2	6.0	745	83	E
82	16-Jun-2008	N1	2.3	537	161	E
83	16-Jun-2008	N1	2.8	575	359	P
84	2-Jul-2008	N1	3.6	632	1	M
85	2-Jul-2008	N1	2.0	525	3	E
86	10-Jul-2008	N1	2.2	524	335	P
87	10-Jul-2008	N1	2.0	526	335	P

Table 2. Instantaneous mortality rates (Z = total mortality, F = fishing mortality, M = natural mortality) of red snapper estimated from telemetry by the Kaplan-Meier, Staggered entry, and Ricker methods. The values in parentheses are 95% confidence limits (CLs). Exploitation = u, expectation of natural death = v.

Method	Parameters	Z	F	M
Kaplan-Meier	n = 70 fish released on day 0	0.50 (0.33–0.76)	0.38 (0.24–0.62)	0.12 (0.05–0.27)
Staggered entry	n = 70 fish staggered release	0.43 (0.32–0.60)	0.31 (0.20–0.46)	0.12 (0.04–0.22)
Ricker model (1)	mean u = 0.25/year (this study) Z = 0.54 (Szedlmayer 2007)	0.54	0.32	0.22
Ricker model (2)	mean v = 0.11/year (this study) Z = 0.54 (Szedlmayer 2007)	0.54	0.40	0.14
Ricker model (3)	mean u = 0.25/year (this study) mean v = 0.11/year (this study)	0.44	0.30	0.14

Table 3. Instantaneous mortality rates (Z = total mortality, F = fishing mortality, M = natural mortality) of red snapper for each full year of the study estimated from telemetry by the Staggered entry and Ricker methods.

Method	Year	M	F	Z
Staggered entry	2006	0.00	0.62	0.62
	2007	0.23	0.24	0.47
	2008	0.17	0.17	0.34
Ricker (model-3)	2006	0.00	0.80	0.80
	2007	0.28	0.25	0.53
	2008	0.20	0.14	0.34

Table 4. Methods used to estimate natural mortality (M) from life history parameters for red snapper in the northern Gulf of Mexico. The following parameters were used: $K = 0.17$, $t_0 = -0.79$, $L_\infty = 92.3$ cm (Szedlmayer 2007); $t_{max} = 52$, $W_{max} = 22790$ g, inAge = 1, finAge = 52 (Wilson and Nieland 2001); $T = 21.5$ °C (mean temperature at 30 m from 1Aug2006–1Aug2008, continuous loggers deployed during this study). The maximum age (t_{max}) = 52 years; estimates of M in parentheses use $t_{max} = 42$ (Szedlmayer and Shipp 1994). The proportion of fish surviving to maximum age is 1% (Ps = 0.01).

Method	Equation	M
Jensen (1996)	$M = 1.5(K)$	0.26
Hoenig (1983)	$\log_e(M) = 1.46 - 1.01 \log_e(t_{max})$	(0.10)
		0.08
Quinn and Deriso (1999)	$M = -\log_e(Ps) / t_{max}$	(0.11)
		0.09
Peterson and Wroblewski (1984)	$M = 1.92(W_{max}^{-0.25})$	0.16
Pauly (1980)	$\log(M) = -0.0066 - 0.279 \log(L_\infty)$ $+ 0.6543 \log(K) + 0.4634 \log(T)$	0.36
Chen and Watanabe (1989)	$M = 1 / (\text{inAge} - \text{finAge})$ $\cdot \log_e\{[e^{(K \cdot \text{finAge})} - e^{(K \cdot t0)}] / [e^{(K \cdot \text{inAge})} - e^{(K \cdot t0)}]\}$	0.20
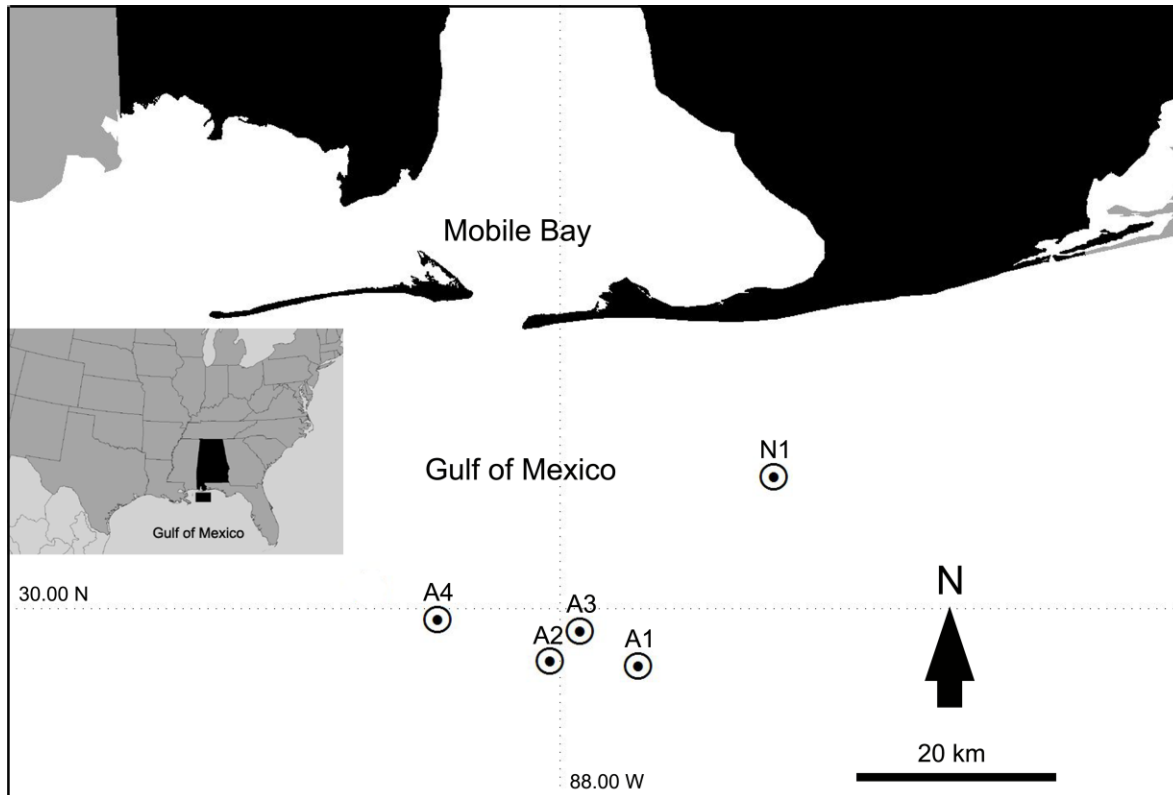
Figure 1. Location of study sites (A1–A4, N1) in the northeast Gulf of Mexico. Inset (middle left) shows Gulf of Mexico and study area (black box) offshore Alabama (black), USA.
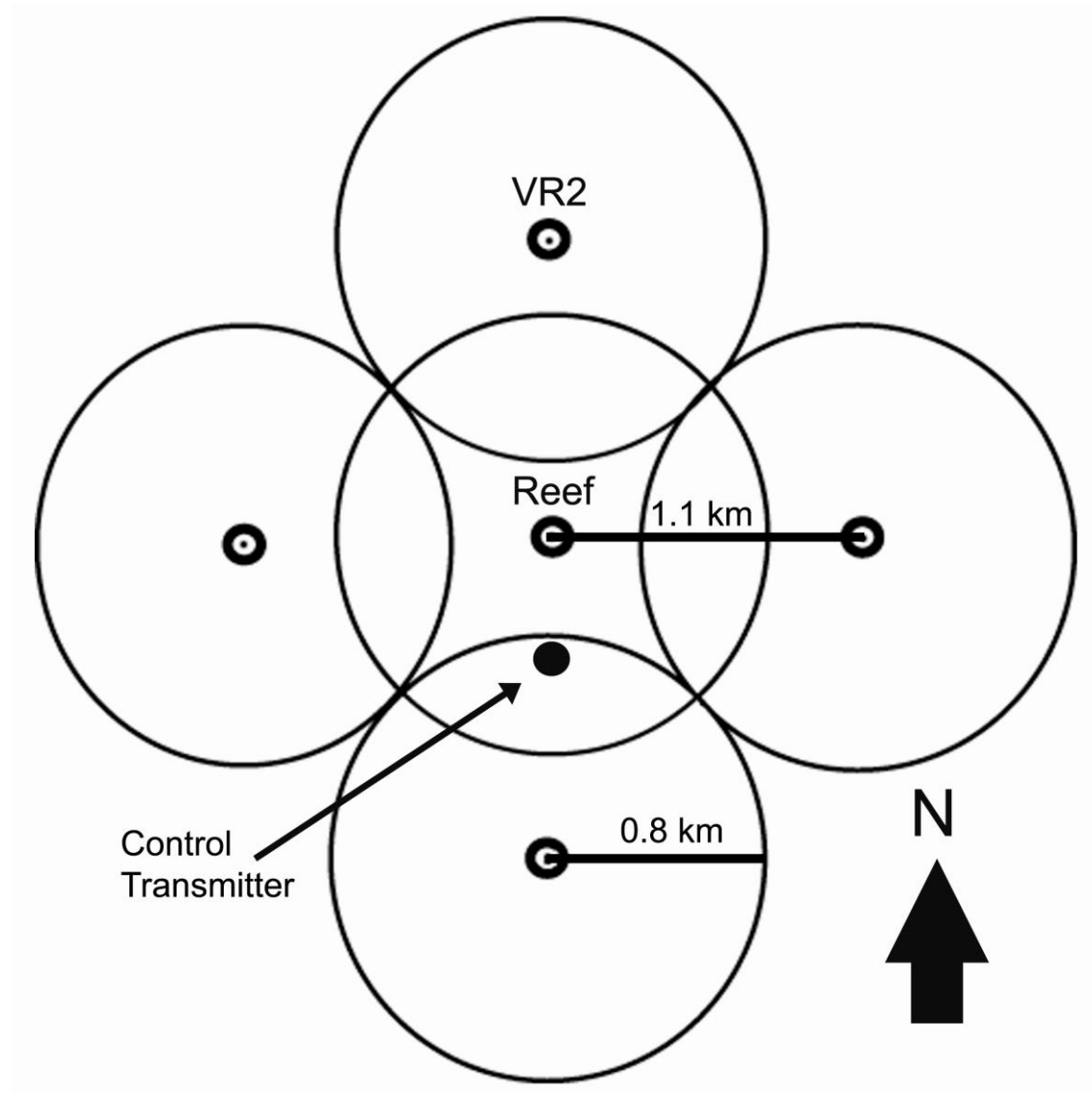
Figure 2. Receiver array design for each site, with one receiver at the reef and four others surrounding the reef 1.1 km (0.4 km at site A4) away to the N, S, E, and W. Circles represent detection range of 0.8 km. A stationary control transmitter was placed 400 m S of reef (150 m at A4).
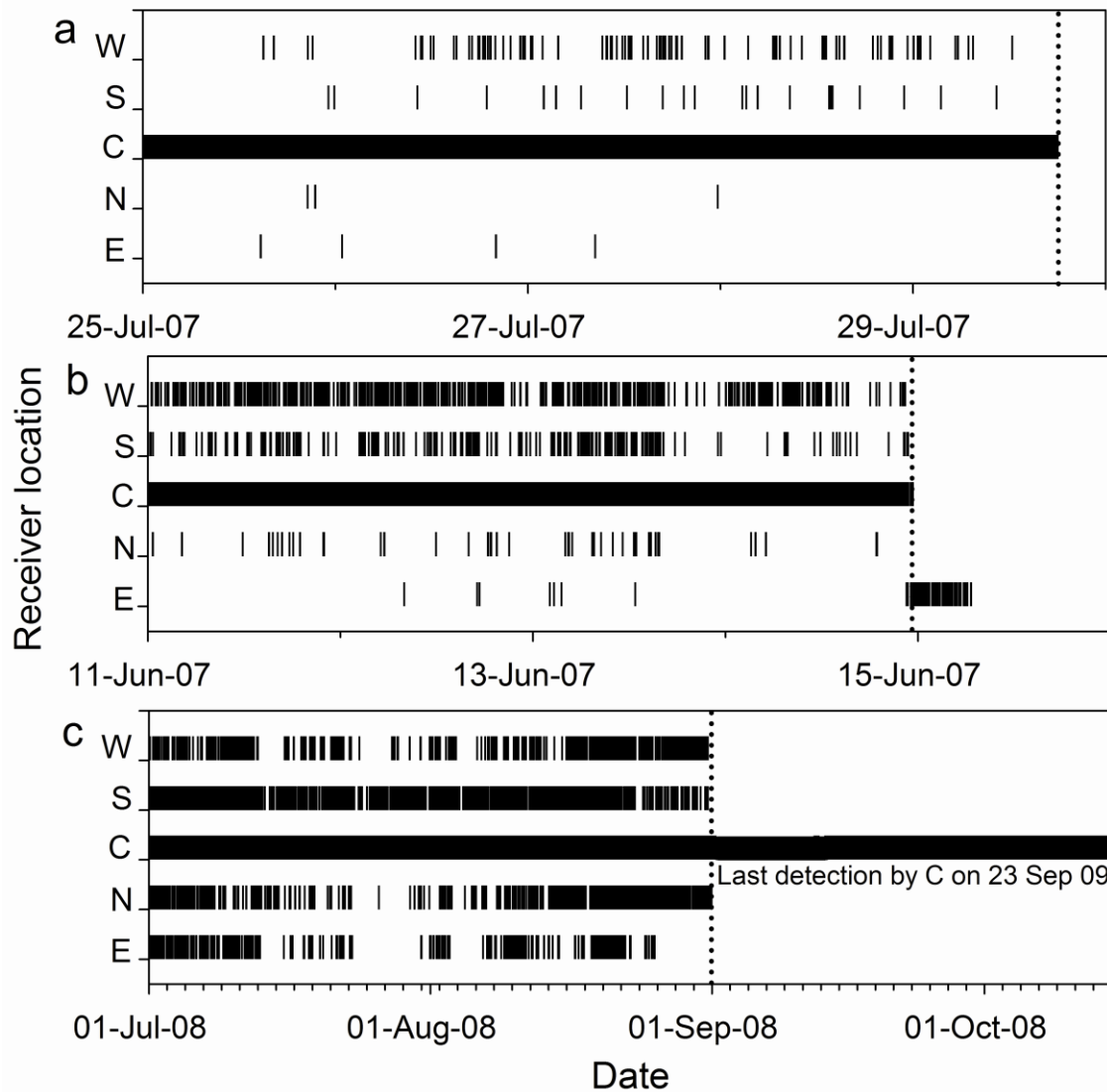
Figure 3. Plots showing examples of the detection patterns expected from fish experiencing either a) fishing mortality, b) emigration, or c) natural mortality events. Each plot shows a segment of the overall detections of a single fish by the Center (C), North (N), South (S), East (E), and West (W) receivers at its site of release. The vertical dashed lines indicate the occurrence of the specified event. Note: different scales for X-axis.
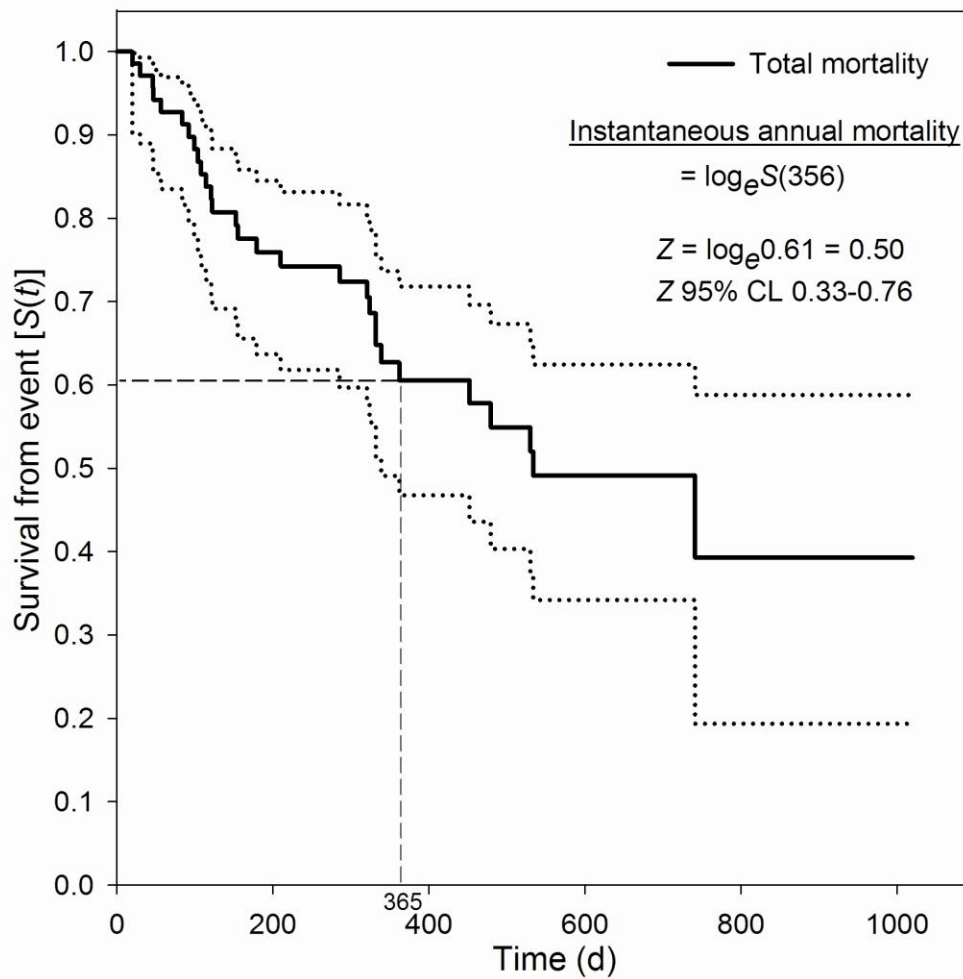
Figure 4. Kaplan-Meier (K-M) estimation of survival (S_Z) of red snapper from total mortality (fishing and natural mortality). Dashed lines show proportion of fish (61%) surviving total mortality at 365 d (*t*). Dotted lines are 95% confidence limits (CL). Instantaneous total mortality (*Z*) is calculated from proportion surviving at 365 d and *Z* 95% CL is calculated from survival at 365 d at 95% CL.
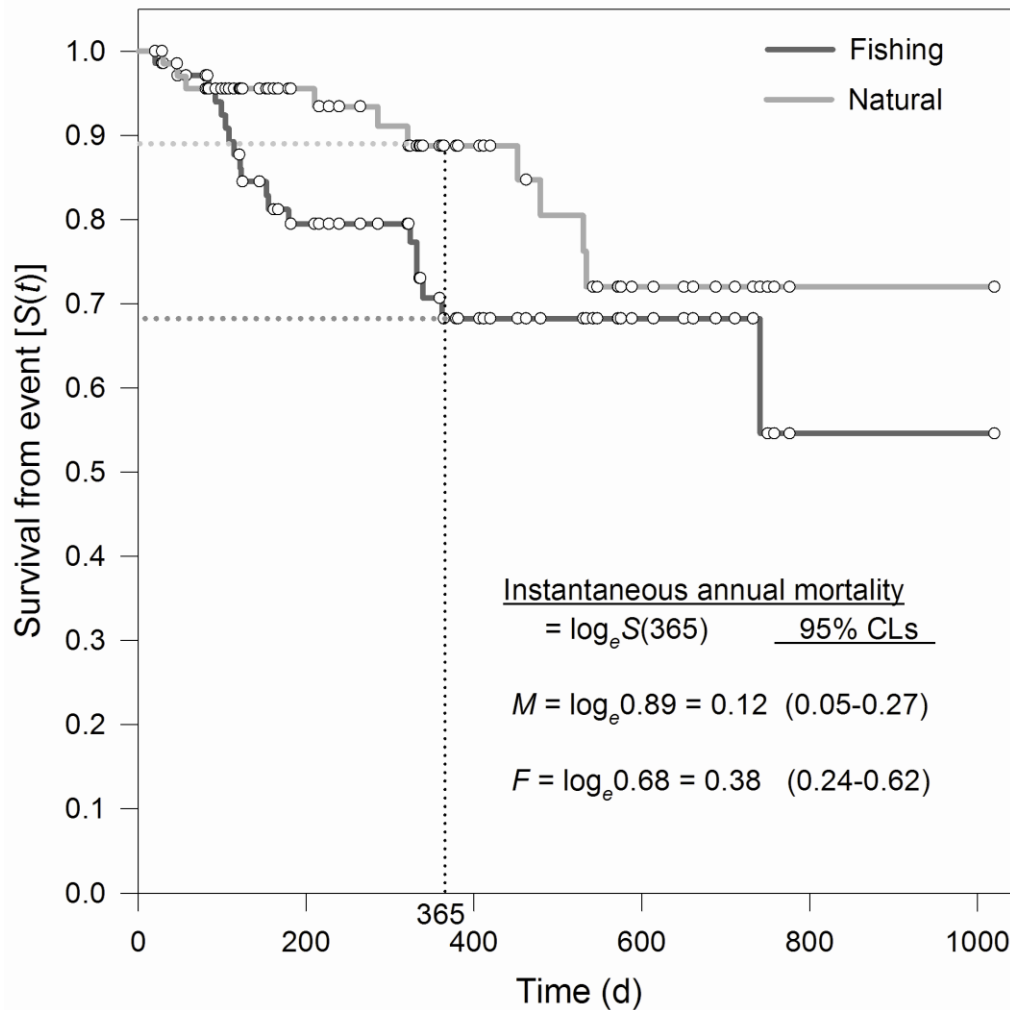
Figure 5. Kaplan-Meier (K-M) estimation of survival (*S*) of red snapper from fishing (dark gray) and natural mortality (gray). Dashed lines show proportion of fish surviving fishing and natural mortality at 365 d (*t*). Instantaneous fishing (*F*) and natural (*M*) mortality rates calculated from proportion surviving each mortality at 365 d and 95% CL is calculated from 95% confidence limits of *S*(365) for each survival probability (not shown).
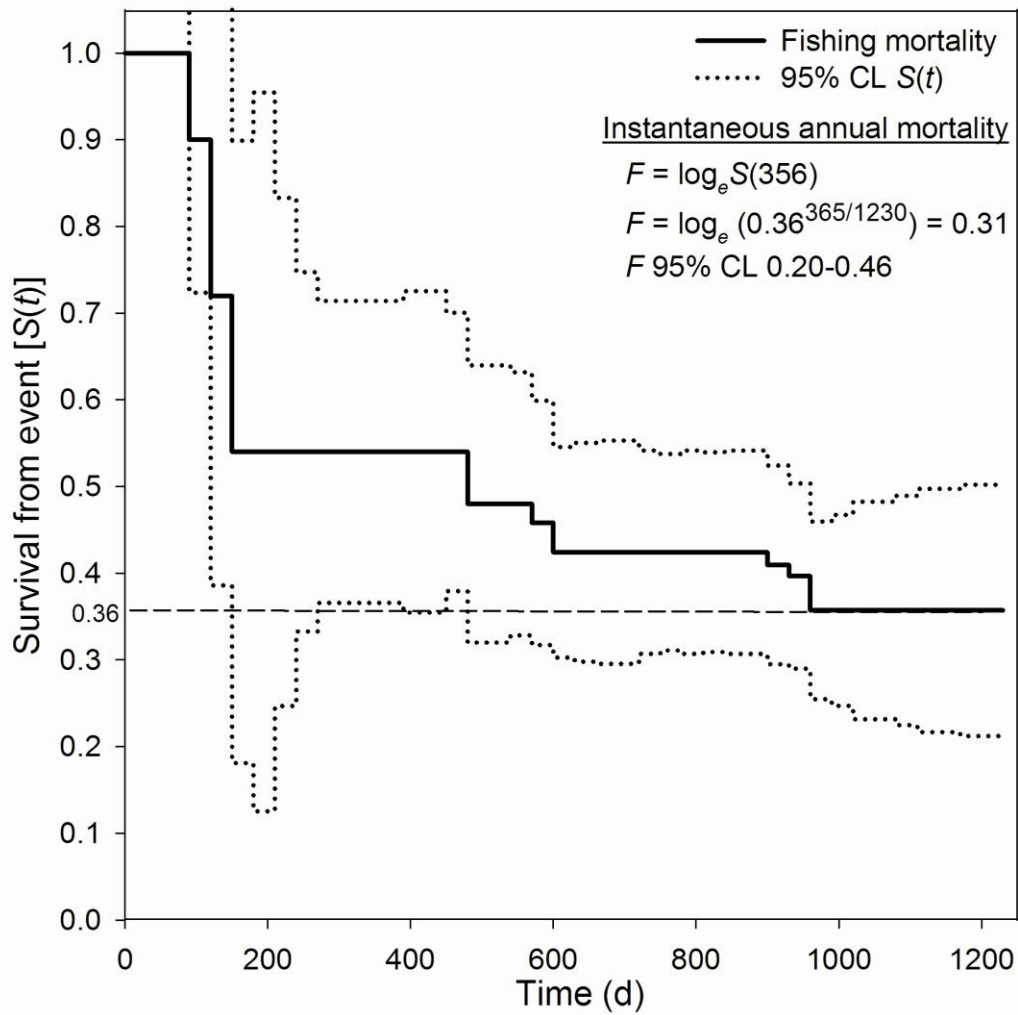
Figure 6. Staggered entry estimation of survival (*S*) of red snapper from fishing mortality.

Dashed line shows proportion (36%) of fish surviving fishing at 1230 d (*t*). Instantaneous fishing

(*F*) mortality rates calculated from proportion surviving at 1230 d, adjusted to $S_F(365) = 74\%$.

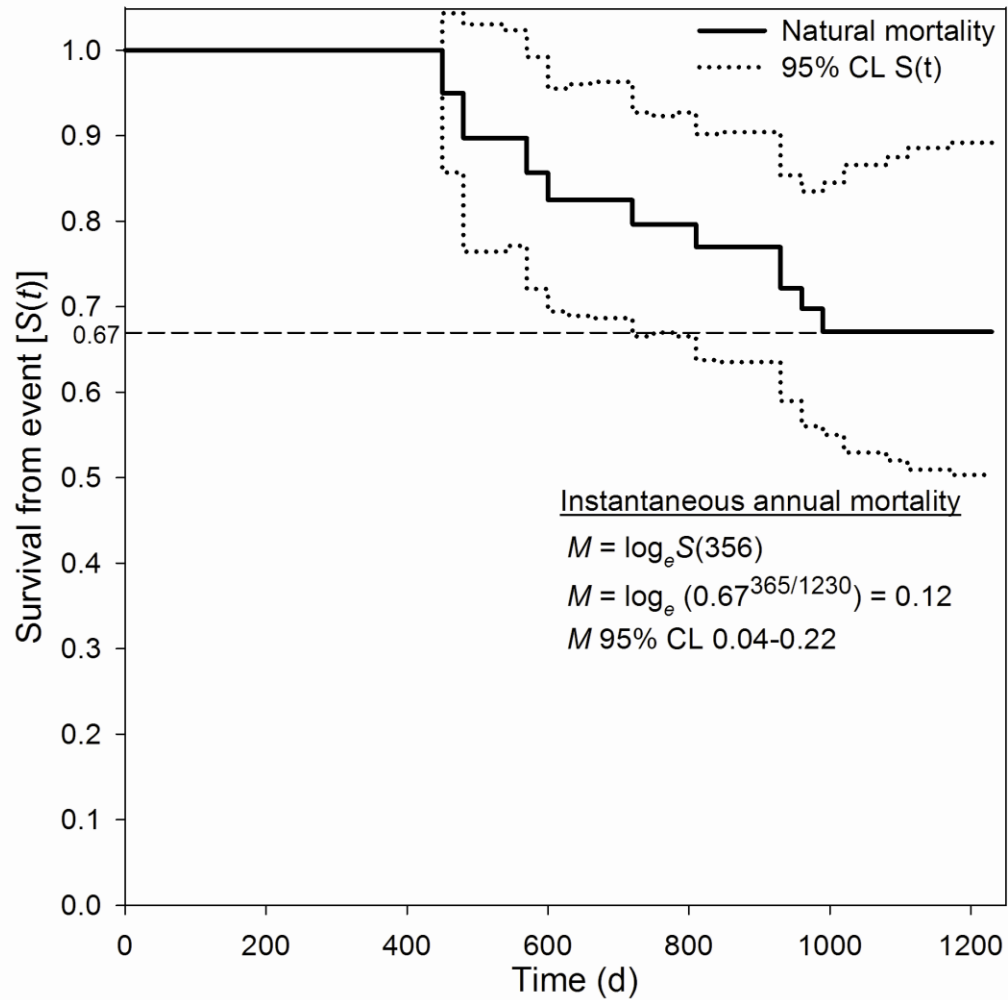Dotted lines are 95% confidence limits (CL). Day 0 is 13 December 2005.

Figure 7. Staggered entry estimation of survival (S) of red snapper from natural mortality.

Dashed line shows proportion (67%) of fish surviving natural mortality at 1230 d (t).

Instantaneous natural (M) mortality rates calculated from proportion surviving at 1230 d,

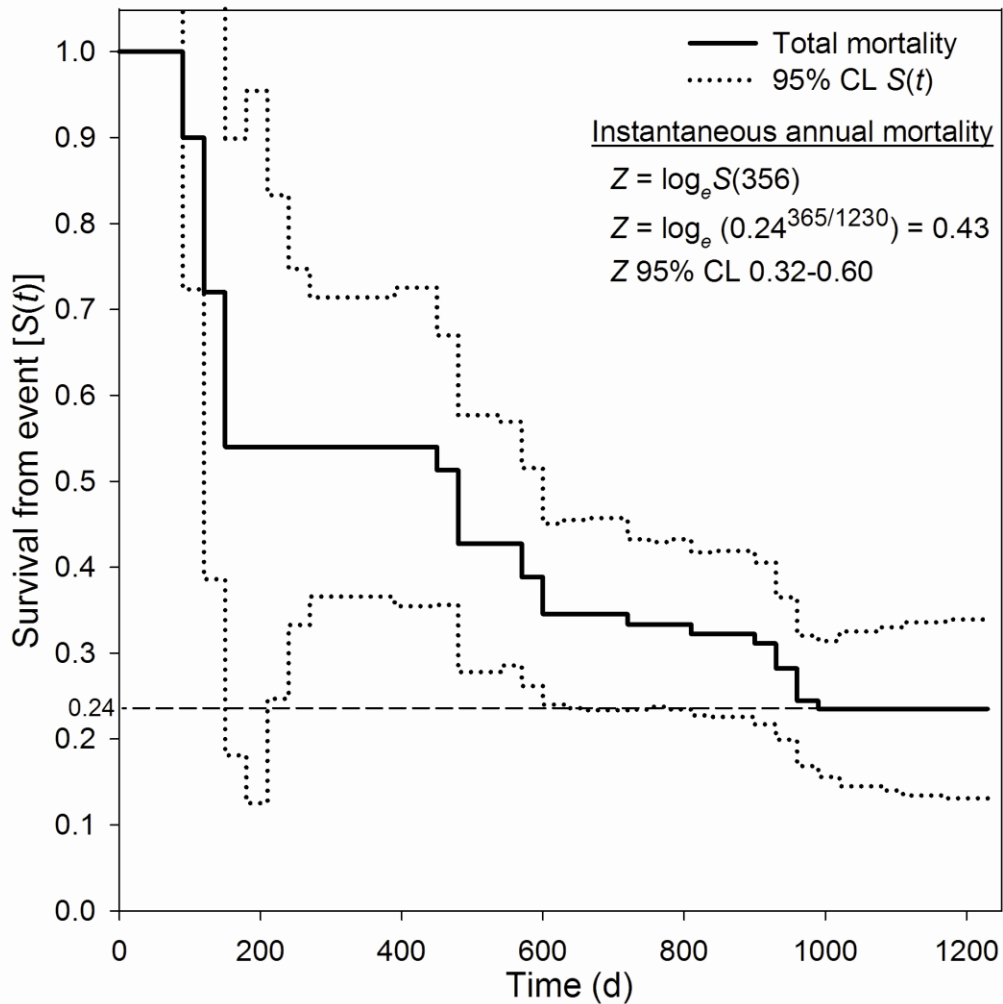adjusted to $S_M(365) = 89\%$. Dotted lines are 95% confidence limits (CL). Day 0 is 13 December

2005.

Figure 8. Staggered entry estimation of survival (*S*) of red snapper from total mortality (fishing

and natural). Dashed line shows proportion (24%) of fish surviving total mortality at 1230 d (*t*).

Instantaneous total (*Z*) mortality rates calculated from proportion surviving at 1230 d, adjusted to

$S_Z(365) = 65\%$. Dotted lines are 95% confidence limits (CL). Day 0 is 13 December 2005.