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Abstract

An accurate estimate of natural mortality (*M*) is critical for the management of any fishery, but is typically difficult to directly measure. Mortality rates for red snapper *Lutjanus campechanus* (N = 87) were estimated from telemetry from December 2005 to June 2009 in the northeastern Gulf of Mexico. At five separate sites an array of five receivers was deployed with one receiver at the center (reef) and four receivers placed 1100 m (or 420 m) north, south, east, and west of center. These arrays enabled the direct estimation of fishing mortality (*F*), natural mortality (*M*), and emigration of acoustically tagged red snapper. Out of the 70 fish that remained at the site for the 6-d recovery period, 19 were caught, 10 died naturally, and 28 emigrated from the 2-km radius study sites. The Kaplan-Meier (K-M) and staggered entry K-M methods were used to estimate survival from different mortality events, and survival was converted to instantaneous mortality rates. Ricker methods were also used to estimate mortality rates. Overall all years combined total mortality (*Z*) ranged from 0.43 to 0.50, *F* from 0.30 to 0.38, and *M* from 0.12 to 0.22. More importantly, *M* estimated for each year changed from 0 in 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 in 2006 to 0.24-0.25 in 2007 and 0.14 – 0.17 in 2008. Thus, in more recent years (2007-2008) *M* may have increased, while *F* may have decreased compared to past estimates (M = 0.1; F = 0.35) used in stock assessments. These higher levels of *M* coupled with the decreasing rates of *F* over 2006 to 2008 suggests that in recent years restrictive management efforts may have accomplished the goal of reaching $F_{SPR26\%}$.

INTRODUCTION

Historically, red snapper *Lutjanus campechanus* have supported important commercial and recreational fisheries in the Gulf of Mexico and are found over both natural and artificial reef habitats (Camber 1955; Moseley 1966; Beaumariage 1969; Bradley and Bryan 1975; Fable 1980; Stanley and Wilson 1989; Szedlmayer and Shipp 1994; Szedlmayer 1997; Watterson et al. 1998; Patterson et al. 2001; Szedlmayer and Schroepfer 2005; Westmeyer et al. 2007). Although approximately 14,000 of these artificial habitats have been built in the northern Gulf of Mexico, possibly enhancing available habitat for this reef oriented species (Minton and Heath 1998; Gallaway et al. 2009), a recent assessment showed that the red snapper fishery was overfished (SEDAR 2009). To rebuild red snapper stocks, managers set an objective of rebuilding stock biomass to a maximum sustainable yield (MSY = 25.4 million pounds) by 2032, which may be accomplished with an instantaneous fishing mortality rate (F) of Fmsy = $F_{\mathrm{SPR}\ 26\%}$ (F at 26 % spawning potential ratio; SEDAR7 2005; DEIS 2006; SEDAR 2009). This objective was based on a conservative assumption of instantaneous natural mortality (M) equal to 0.10/year; however, if M was actually higher, the goal of MSY may be achieved in a shorter period of time (Goodyear 1995; Schirripa and Legault 1999; Slipke and Maceina 2005). Therefore, to allow for an appropriate fishing level for red snapper in the northern Gulf of Mexico, it is important to obtain an accurate estimate of M.

The red snapper fishery has continued for well over a century, and like most exploited fish stocks, the level of M for red snapper in the Gulf is not well defined (Camber 1955; Schirripa and Legault 1999). Total mortality (Z) has been obtained for red snapper from fishery independent catch curve analysis (Gitschlag et al. 2003; Szedlmayer 2007); however, the separation of *Z* into its components of *M* and *F* has been difficult. Estimates of *M* for red snapper have been primarily derived from life history parameter equations based on maximum age, Von Bertalanffy growth coefficient *K*, and water temperature, with estimates of *M* for red snapper ranging from 0.02 to 0.40, with 95% confidence intervals from 0.02 to 1.0 (Alverson and Carney 1975; Pauly 1980; Nelson and Manooch 1982; Hoenig 1983; Goodyear 1995; Schirripa and Legault 1999). The presently applied value of *M* (0.10) is based on maximum ages of red snapper around 40 to 50 years (Hoenig 1983; Szedlmayer and Shipp 1994; Schirripa and Legault 1999; Wilson and Nieland 2001; SEDAR7 2005). This value of *M* (0.10) is conservative when compared to estimates of *M* based on other life history parameters. This uncertainty in *M* has lead to cautious management practices and severe reductions in fishery quotas (Hood et al. 2007). Despite its critical importance in population assessment, direct estimates natural mortality for red snapper have not been reported in the literature.

Recent advances in telemetry systems, such as continuous automated monitoring, long-life transmitters, and long distance detection, have allowed researchers to directly estimate natural and fishing mortality in both fresh and saltwater environments (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pine et al. 2003; Pollock et al. 2004; Young and Isely 2004; Starr et al. 2005). With these advances in technology, estimates of mortality are possible for species like red snapper that inhabit large open water systems. In this study, strategic placement of remote telemetry receivers allowed separation of total declines in tagged fish into its component parts of emigration, natural mortality, and fishing mortality.

METHODS

Study Area

The study sites were located 20 to 30 km south of Mobile Bay, Alabama, USA, an area that includes numerous artificial habitats (> 10,000) and a few natural rock-reef habitats (Schroeder et al. 1988; Minton and Heath 1998). Red snapper were tagged on one natural and four artificial habitats. Artificial habitats included a pipeline covered with a concrete mat (A1), a 15-m sunken 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 habitat site (N1) was composed of a 20-m long drowned river bed (~1 m high, ~5 m apart), with undercut banks lined with tree stumps (Figure 1). Depths of the sites ranged from 20–30 m. These sites were a mix of public (published latitude longitude) and private locations (Figure 1).

Fish Tagging

Red snapper (> 500 mm total length [TL]) were captured at the sites via hook and line, and tagged with ultrasonic transmitters (Szedlmayer and Schroepfer 2005). Fish were placed in a 70-L container of seawater containing MS-222 (150 mg MS-222/L seawater), and quickly anesthetized (level 4; Summerfelt & Smith 1990). Fish were weighed and measured, and an ultrasonic transmitter was implanted through a small (18 mm) vertical incision into the peritoneal cavity with a No. 11 scalpel slightly above the ventral midline, and then sutured with plain gut suture (Ethicon, no. 2, 3.5 metric). An internal anchor tag (Floy) was also inserted into the incision before it was sutured. Sterile surgical methods and betadine were used throughout the procedure. The fish were released after being held at the surface for a short (~1 min) recovery period (when strong fin and gill movements were observed). Fish were released at the capture site by lowering fish to the bottom with weighted line with an inverted barbless hook that was attached to the fish's lower jaw. Retrieval of the weighted line released the fish at the bottom near the reef.

Two types of transmitters were used for this study. Individually coded Vemco transmitters (V16-6L-R64K; code intervals: 20 to 69 s, 16 x 94 mm, battery life: 6 years) were used at sites with Vemco VR2 receivers, and Sonotronics transmitters (CT-05-48; continuous, 16 x 79 mm, battery life: 4 years) were used at site A4 with Sonotronics SUR-1 receivers. Maximum detection ranges were 1600 m for Vemco and 600 m for Sonotronics transmitters. The effects of transmitter implantation on behavior or health of red snapper were assumed to be negligible after a 6 d recovery period, because transmitter weights were < 2% of the total body weight of the fish (Winter 1983; Adams et al. 1998; Brown et al. 1999).

Continuous Remote Monitoring

An underwater acoustic receiver array was deployed at each site that included five separate omni-directional receivers (Vemco VR2 or Sonotronics SUR) moored ~5 m above the bottom. For each array, one receiver was located at the release site [Center (C)] and the other four were placed at 1100 m (VR2) or 420 m (SUR) to the North (N), South (S), East (E), and West (W) of the center (Figure 2). Receivers placed at 1100 m (or 420 m) away from the center receiver were predicted to result in complete detection of the fish within a ~2 km (VR2) or 1-km (SUR) radius of the release sites (Szedlmayer and Schroepfer 2005). Receivers were coated with copper based antifouling paint to prevent possible signal occlusion due to biofouling (Heupel et al. 2008).

Detection patterns of fish by these arrays identified if a fish was caught (fishing mortality), died (natural mortality), or emigrated. Fishing mortality was also estimated from tag returns by fishers. For example, a fishing mortality was identified by a detection pattern that would show consistent, continuous detections at the center site, followed by a sudden loss of detections at time of capture. Emigration was shown as a decrease in detections of a fish at the center site followed by an increase in detections at a surrounding receiver prior to complete detection loss. A natural mortality was identified when a fish stopped being detected at any outside receiver but was still detected by the center receiver. This natural mortality detection pattern resulted from a lack of fish movement and decrease in detection range from a transmitter that was lying on the bottom. Each site was periodically surveyed with SCUBA divers, aided with a hand-held receiver, to visually identify live fish with external tags and transmitters, and search for stationary transmitters laying on the substrate from fish mortalities. A stationary control transmitter was placed 400 m (VR2) or 150 m (SUR) south of the center location at each site to estimate changes in detection range throughout the study, and enabled contrasts between movements and mortality (Topping and Szedlmayer 2011a).

Estimates of Mortality

Several methods were used to calculate mortality rates, including equations defined by Ricker (1975), Kaplan and Meier (1958), and Pollock et al. (1989).

Ricker method.–Annual exploitation rates (*u*) were derived from tag returns and telemetry-identified fishing mortalities. Exploitation rates were calculated each month as the number of tagged fish captured that month out of the number of tagged fish at risk of being captured at the start of that month. The number of fish at risk at the start of each month was calculated as the fish present at the start of the previous month minus all mortalities (fishing and natural) plus new fish released during the previous month. An adjustment was made to the number of fish at risk that accounted for non-reporting and natural mortalities of fish that emigrated from the sites. The adjustment was based on the rates (proportion) of fisher non-reporting and natural mortality estimated for fish that remained at the sites, and assumes that fish emigrating will incur the same mortality rates as fish remaining within the receiver detection range at a site. A mean yearly rate was calculated by multiplying the mean monthly u by 12. Expectation of natural death (v) was calculated monthly from telemetry-detected natural mortalities at each site, and is defined as the number of tagged fish dying naturally that month out of the number of tagged fish at risk of dying at the start of that month. The number of fish at risk of dying at the start of each month was calculated as the fish present at the start of the previous month minus all mortalities (fishing and natural) plus new fish released during the previous month. Also, all fish that emigrated the previous month were removed from the fish at risk so that natural death rate was only calculated for fish remaining at the site, because natural mortality could not be detected for fish that emigrated. To estimate annual rates of instantaneous fishing mortality (F) and natural mortality (M), two estimates of instantaneous total mortality (Z) were applied. Total mortality (Z) was estimated from the present telemetry derived estimates of u and v, and from catch-curve analysis in previous studies (Z = 0.54; Gitschlag et al. 2003; Szedlmayer 2007). Annual survival (S) was either calculated from the catch-curve or from u and v.

Three separate models were used to estimate M and F (Ricker 1975). Ricker model (1), where $F = u\,Z\,/\,(1 - S)$ was used to calculate F from the telemetry-based u and the catch curve derived $Z = 0.54$ (with $S = e^{-Z}$), then M was estimated by subtraction ($M = Z - F$). Ricker model (2), where $M = v\,Z\,/\,(1 - S)$ was used to calculate M from the telemetry-based v and the catch curve derived Z = 0.54 (with $S = e^{-Z}$), then F was estimated by subtraction ($F = Z - M$). In Ricker model (3), both M and F were calculated separately from telemetry-based estimates of u, v, and Z, using Ricker models (1) and (2), with $S = 1 - (u + v)$ and $Z = \log_e(S)$.

Kaplan-Meier method.–Mortality rates were calculated from the survival function, $S(t)$, estimated from the product limit method of Kaplan and Meier (1958), which gives the probabilities (S) of surviving a specified event (i.e. fishing, natural, or total mortality) over a given time (t). This method allows for removal (right-censor) of fish that were not subject to the particular mortality under analysis. For example, when estimating survival from natural mortality events, fish caught and fish that emigrate from the site are censored from the analysis at the point of that event occurring (i.e. fish did not experience a natural mortality up to the time of the emigration or capture and are no longer at risk of a natural mortality). The Kaplan-Meier (K-M) event analysis method was applied using the survival function:

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

the probability of surviving to t, where t is the time over which survival is estimated from the product of the conditional probabilities of survival at each event point j, and where d_j represents the number of individuals experiencing an event and r_j represents the number of individuals at risk of an event at time t_j (Kaplan and Meier 1958; Allison 1995; Schroepfer and Szedlmayer 2006).

The SAS Lifetest procedure was used to estimate the survival to t assuming fish are released on the same day and examines the entire distribution of event and censor times (Allison 1995). Survival was then estimated at 365 days. By analyzing event times with respect to the same start date, the effects of low sample size (in the beginning of the study) on K-M survival estimates are removed. Survival functions were estimated separately for M, F, and Z. For example, for survival from fishing mortality (event), fish that emigrated and died naturally were right censored from the fish at risk. In this method, individuals censored are assumed to have the same prospect of survival as individuals remaining at the study site. Since survival estimates are independently derived by only considering the specified mortality event, instantaneous annual mortality rates were calculated using the following equations:

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

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

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

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

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

where survival is based on probability of surviving any mortality over a year. Variances for K-M survival estimates were defined by Cox and Oakes (1984) as

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

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

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

Ranges of mortality rates were calculated from the 95% confidence interval ranges of the survival functions at a time of 365 d.

Staggered entry method.–The staggered entry method is a modification of the previous K-M survival function method and has been applied to telemetry data (Pollock et al. 1989; Heupel and

Simpfendorfer 2002). The staggered entry equation is similar to the K-M, with the exception that this method allows individuals to enter at any time during the study. Individuals that emigrated or did not experience the specified mortality event over the given time period were right censored as discussed above (e.g., a fish emigrating 200 d after release was known to survive a mortality event for at least 200 d). In the staggered entry method, the number of fish at risk could fluctuate from period to period depending on the number of fish present, new releases (additions), and removals from the sites (fishing mortality, natural mortality, and emigrations) in the previous period. The survival function was estimated by taking the product of the conditional survival probabilities calculated every 30-d period up to the 1230-d study length (i.e. 42 time periods). The mortality rate equations were adjusted to estimate an annual survival $S(365)$ from the survival probabilities at the end of the study $S(1230)$ by applying an exponent of 365/1230 (e.g. F, M, or $Z = -\log_e[S(1230)^{365/1230}]$; Starr et al. 2005).

RESULTS

Red snapper (N = 87) were continuously monitored at five different sites (A1-A4, N1; Figure 1) for 1230 d (December 2005 to May 2009). Total length (TL) of tagged red snapper ranged from 501 to 860 mm, with a mean of 639 mm (SD, 85 mm). These 87 fish remained present at the site, emigrated, died, or were removed by fishers, as determined by detections from the five receivers at each site and by fisher returns (e.g. Figure 3; Table 1). Event times (or minimum residence time if still present) ranged from 0 to 1020 d (Table 1). Of the 87 tagged fish, 17 either left the site or died within the first 6 d after release (14 emigrated, 2 died, and 1 unknown). These events within the first 6 d post release were considered tagging artifacts, and no fish that left within 6 d were detected again or returned by fishers. Thus, the 70 remaining fish were used for mortality rate estimations, and data were analyzed up to 27 May 2009 (just prior to the 2009 fishing season).

There were 14 fish still present at the various sites at the end of the study (Table 1). Additional emigrations were detected (n = 27) after the 6-d post-release period, with 2 fish in 2006, 9 fish in 2007, 14 fish in 2008, and 2 fish in 2009 leaving the site from 28 to 758 d after release. Six fish from the 27 emigrations were last detected at a site when one of the five outer array receivers was not functioning, but were assumed to have emigrated based on the detections from other receivers at that site (unknowns [U]; Table 1). No natural mortalities were detected in 2006, but there were five in 2007, five in 2008, and none in 2009 (up to June 2009). There were 19 fishing mortalities at four sites (A1-A4, F = 0 at N1), with 17 fish returned by fishers and 2 estimated from telemetry detection data. Nine fish were caught in 2006, five in 2007, and five in 2008. Of the nine fish caught in 2006, all were caught at site A1 in April, May, and June, and six were captured by one fisher. This fisher admittedly targeted this site. Overall, site A1 had the highest fishing mortality (13 fish out of 20 released). Targeting of this study site may have increased exploitation rates beyond actual levels in 2006 (u = 0.50, April; 0.75, June), as few fish were at risk during the early part of this study (10 fish in April, 5 in May, and 6 in June). Both the Ricker and staggered entry models are sensitive to low sample sizes in the beginning of the study which resulted in negative or zero M values, and F values greater than 1.0. Because of the fishing mortality bias from this particular fisher, these captures were censored in the Ricker and right censored in the staggered entry analysis, and not included in the fishing mortality estimates for these models, but the mortalities from this directed fisher were included K-M mortality estimates.

Ricker Mortality Estimates

The mean yearly exploitation rate (*u*) was 0.25/year (SE, 0.12). The *u* decreased each year, from 0.55/year (2006) to 0.19/year (2007) to 0.12/year (2008). The fisher capture reporting rate was > 90% based on detections and tag returns, with only 2 fish out of 19 not returned by a fisher. Natural death rate (*v*) over all sites was 0.11/year (SE, 0.04). No natural mortality was detected in 2006, *v* was 0.22/year in 2007, and 0.17/year in 2008.

The Ricker model (1) mortality estimates were $F = 0.32$ and $M = 0.22$ (from subtraction), based on a Z of 0.54 (Gitschlag et al. 2003; Szedlmayer 2007) and $u = 0.25$/year (Table 2). The Ricker model (2) mortality estimates were $M = 0.14$ and $F = 0.40$ (from subtraction), based on the same $Z = 0.54$ and $v = 0.11$/year (Table 2). Ricker model (3) mortality estimates were $F = 0.30$ and $M = 0.14$, based on estimates of $u = 0.25$/year, $v = 0.11$/year, and $Z = 0.44$ from the present study (Table 2). Ricker model (3) was used to obtain mortality estimates by year from above yearly estimates of *u* and *v*. In 2006, $F = 0.80$ and $M = 0.0$; in 2007, $F = 0.25$ and $M = 0.28$; and, in 2008, $F = 0.14$ and $M = 0.20$ (Table 3).

Kaplan-Meier Mortality Estimates

The estimation of mortality rates using the Kaplan-Meier (K-M) method were based on all data ($n = 70$ fish). All fish were considered to be released on the same start date, and as such there was not artificial inflation of mortality rates when few fish were at risk at the beginning of the study. The overall rate of survival (*S*) from all mortality (fishing + natural) was 61% at 365 d (S_Z[365]) or Z = 0.50 (Table 2; Figure 4). When survival from fishing mortality was estimated, S_F(365) = 68% and F = 0.38 (Table 2; Figure 5). When survival from natural mortality was estimated, S_M(365) = 89% and M = 0.12 (Table 2; Figure 5). If the K-M method was applied with the recaptures from the fisher that targeted site A1 removed (right censored), Z = 0.39 and F = 0.27.

If the K-M method is applied to only 2007 and 2008 data (n = 44 fish), F would also decrease from 0.45 to 0.31, but this would exclude most of the fish released at site A1. Site A1 had the most fishing mortalities (13 of 20 fish), and was the first site established. If all sites except A1 were considered (n = 50 fish), F would be 0.20; however, if F was based only on site A1, F would be 1.0. Site A4 had the second highest F (0.56), and was a public site. Site N1 was the last site established (December 2007), and showed the lowest F = 0, compared to other sites.

Staggered Entry Mortality Estimates

The staggered entry method also showed sensitivity to low sample size in the beginning six months of this study as shown in the Ricker method. After the first six months (June 2006), the probability of survival (i.e., S_F[180]) dropped to 10% when all fishing mortalities were considered, resulting in an F of 2.3, which is an unrealistic estimate. After removal of the captures from the biased fisher, fishing mortality decreased, S_F(365) = 74% and F = 0.31 (Table 2; Figure 6). While no natural deaths were detected in 2006 (probably due to low sample size), natural deaths were spread out relatively evenly in subsequent years. Survival from a natural mortality using the K-M staggered entry was S_M(365) = 89%, M = 0.12; and, survival from all mortality was $S_Z(365) = 65\%$, Z = 0.43 (Table 2; Figure 7, 8). Mortality rate estimates based on the staggered entry method varied by year (Table 3).

DISCUSSION

Ultrasonic telemetry allowed continuous, long-term (~ 3 years) monitoring of tagged red snapper at the study sites. The arrangement of receivers enabled the estimation of emigration, natural mortality, and fishing mortality at various habitat structures. An important advancement in the present study was the use of stationary control transmitters at each site that allowed monitoring detection range changes due to environmental factors throughout the study. Knowledge of detection range and comparisons between detection patterns of stationary (dead fish) and moving (live fish) transmitters were necessary for identifying emigration and mortality events (Topping and Szedlmayer 2011a). Most studies that employed telemetry techniques to estimate mortality of relatively mobile species (e.g., striped bass, blacktip sharks) have been successful in semi-closed systems and generally have estimated natural mortalities based on lack of movement (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Young and Isely 2004). For example, Heupel and Simpfendorfer (2002) were able to directly detect fishing and natural mortality of juvenile blacktip sharks in Terra Ceia bay by using a large number of VR2 receivers to continuously monitor movement, lack of movement (mortality), sudden disappearance (capture), and emigration of individuals from the mouth of the bay. More difficulty is encountered when attempting to estimate mortality with telemetry in open ocean systems (vs closed), and has been limited to fish that show moderate residence (Starr et al. 2005). In the present study, high site fidelity of red snapper to reef sites (Szedlmayer and schroepfer 2005;

Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a, b) provided an opportunity to directly estimate mortality rates and emigration of red snapper for the first time in a large open water system (i.e., northern continental shelf of the Gulf of Mexico).

Values of *F* for some stock assessments are dependent on *M*, in which *M* is determined indirectly from the life history parameter equations, with *F* only as accurate as *M* (Manooch et al. 1998). Estimates of *M* derived indirectly from life history parameters for red snapper from the northern Gulf of Mexico (Table 4; e.g. maximum age, maximum weight, *K*, water temperature) can range from 0.08 to 0.36 (Chen and Watanabe 1989; Pauly 1980; Hoenig 1983; Peterson and Wroblewski 1984; Jensen 1996; Quinn and Deriso 1999; Slipke and Maceina 2005; Wilson and Nieland 2001; Szedlmayer 2007). The most recent red snapper fishery assessment used a conservative *M* of 0.10, which was lowered from the 0.20 used in an earlier assessment (Goodyear 1995; Schirripa and Legault 1999; SEDAR7 2005; SEDAR 2009). The predicted *M* was lowered due to evidence of older fish (up to 53 years) in the stock (Szedlmayer and Shipp 1994; Schirripa and Legault 1999; Wilson and Nieland 2001). Over all years combined the direct estimates of *M* from telemetry methods in this study (0.12–0.22; 95% CL = 0.04–0.27; Table 2) were consistent with estimates from the indirect methods (0.08–0.36; Table 4), but higher than the estimate of *M* used in the most recent assessment (0.10). The present study provides the only empirically derived estimates of *M* for red snapper, however such estimates will probably change from year to year depending on environmental conditions or from possible increases in density-dependent mortality associated with population increase during the red snapper stock rebuilding phase (Rose et al. 2001; Gazey et al. 2008).

Detection of changes in natural mortality rates among years or shorter periods of time (Young and Isely 2004) or during catastrophic environmental conditions (e.g. hurricanes or dead zones) could be efficiently assessed with the present telemetry methods. There were no natural deaths detected in 2006 probably due to the combination of low sample size and the high number of released fish caught by fishers early in the study. In the following years, M was higher based on the staggered entry method (0.23 in 2007; 0.17 in 2008). The Ricker model-3 also showed higher estimates of in 2007 (M = 0.28) and 2008 (0.20) than 2006 (0). We suggest that these later estimates of M (0.17 to 0.28) are probably better estimates of actual red snapper natural mortality rates, because of greater sample size and reduced fishing mortality.

Over all years combined the direct estimates of F in this study (0.30–0.40; 95% CL 0.24–0.64) were similar to F = 0.35 for red snapper from the 2005 stock assessment (SEDAR7 2005) and F = 0.29 to 0.47 from the 1999 stock assessment (Schirripa and Legault 1999). However, F showed substantial annual variation during this study. The higher exploitation rates in 2006 for the present study may be lower sample sizes inflating exploitation, but also may reflect changes in fishing regulations among years. Total allowable catch (TAC) quotas were decreased from 9.1 million pounds (MP) in 2006, to 6.5 MP in 2007, and to 5.0 MP in 2008. These reductions in TAC resulted in more restrictive seasonal and bag limits. For example, in 2006 the federal waters were open to recreational red snapper fishing for seven months (April to October 2006) with a four fish bag limit (407 mm TL minimum size), in 2007 a two fish bag limit was instituted, and in 2008 the fishing season was limited to two months (June and July 2008). Though it is difficult to compare the first year of the study due to low sample size, the decreasing pattern of fishing mortality from 2006 to 2008 in the present telemetry study appeared to reflect the changes in fishery management regulations. Fishing mortality (*F*) was 0.80 in 2006, 0.25 in 2007, and 0.14 in 2008 (Ricker model 3).

Detection of a fishing mortality event based on telemetry detection data was validated by fisher returns (*n* = 17 fisher returns out of 19 telemetry detected fishing mortalities). Confidence in the accuracy of detection of *M* was < *F* since we were not able to retrieve all of the transmitters from dead fish. However, even when independently estimating each type of mortality event, there was a convergence of mortality rates estimated among the various methods (low variability), which increases confidence in the accuracy of *M*. Total mortality (*Z*) estimates showed low variance among the methods used, with estimates of 0.50 (K-M), 0.43 (staggered entry), and 0.44 (Ricker model 3), which are similar to a *Z* of 0.54 obtained by both Gitschlag et al. (2003) and Szedlmayer (2007) from catch curves of completely separate fishery independent surveys. Although the different methods of estimating mortality showed similar results, there were advantages and disadvantages of each method. The staggered entry (modified K-M; Pollock et al. 1989) and K-M methods simplify calculations, with only data needed on the time from release till an event, an emigration, or if a fish is still present. The staggered entry method is suggested as the preferred method if there is a reasonably high initial release of individuals into the study, and this method allows for additional individuals to be added throughout the study (Heupel and Simpfendorfer 2002). Also, this would be the best method to show seasonal or yearly fluctuations in survival if there are similar sample sizes among periods. The confidence intervals used for the staggered entry method narrowed as the study progressed because sample size increased as more fish were released over the study. The K-M method was the least sensitive to fluctuations in sample size and periods of high mortality. The K-M method showed narrower

95% confidence limits in the beginning of the study due to the “release” of all fish (*n* = 70) at day 0. Accuracy of this method is affected by the length of the study, with confidence increasing as more fish progress through the study to experience an event.

The traditional Ricker (1975) methods using *u* or *v* rates and some estimate of *Z* to calculate *F* or *M*, were similar to the staggered entry method. The same time periods (30 d) were used to estimate *u* and *v* (Ricker), and survival (staggered) with similar numbers of fish at risk at the beginning of each period. Since the estimates of *F* may have been more accurate (than *M*) due to validation of detection data with fisher returns, Ricker model 1 (*u* = 0.25/year, *Z* = 0.54) may give the most accurate estimate of *M* (0.22). Again, the major disadvantage with the Ricker method is overestimating exploitation rates when few fish are at risk, as in the beginning of this study.

Since *M* represents a measure of the longevity and natural rate of replacement of the population, higher values of *M* may allow for higher catches in the fishery; however, if the fishery is managed assuming a high *M* when its value is much lower, there may be significant problems (Schirripa and Legualt 1999; Slipke and Maceina 2005). Over all years combined the natural mortality rates estimated in this study (0.12–0.22) were slightly above to more than double the *M* = 0.10 used in past red snapper fishery assessments. More importantly, *M* estimated for each year changed from 0 in 2006, to 0.23-0.28 in 2007 and 0.17-0.20 in 2008. Thus, the present study suggest that natural mortality is higher than past estimates, and may have actually increased to as much as three times the past rates used in stock assessments during the red snapper rebuilding period under restrictive management. This higher level of *M* coupled with the decreasing rates of *F* in 2007 (0.24-0.25) and 2008 (0.14-0.17) suggests that the goal of

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

REFERENCES

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile chinook salmon. Transactions of the American Fisheries Society. 127:128–136.

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

Alverson, D. L., M. J. Carney. 1975. A graphic review of the growth and decay of population cohorts. Journal du Conseil International pour l'Exploration de la Mer 36:133–143.

Beaumariage, D.S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. Florida Department of Natural Resources Technical Series 59:1–38.

Bradley, E., and C. E. Bryan. 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the Northwestern Gulf of Mexico. Gulf and Caribbean Fisheries Institute 27:77–106.

Brown, R. S., J. C. Steven, W. G. Anderson, and R. S. McKinley. 1999. Evidence to Challenge the ‘‘2% Rule’’ for Biotelemetry. North American Journal of Fisheries Management 19:867–871.

Camber, C. I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Florida Board of Conservation Technical Series 12:1–64.

Chen, S., and S. Watanabe. 1989. Age dependence and natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi 55:205–208.

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

DEIS. 2006. Draft environmental impact statement to evaluate alternatives to set Gulf of Mexico red snapper total allowable catch and reduce bycatch in the Gulf of Mexico directed and shrimp trawl fisheries. NOAA, NMFS, St. Petersburg, Florida USA.

Fable Jr, W. A. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the South Texas coast. Contributions in Marine Science 23:115–121.

Gallaway, B. J., S. T. Szedlmayer, and W. J. Gazey. 2009. A life history review for red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Reviews in Fisheries Science 17:48–67.

Gazey, W. J., B. J. Gallaway, J. G. Cole, and D. A. Fournier. 2008. Age composition, growth, and density–dependent mortality in juvenile red snapper estimated from observer data from the Gulf of Mexico penaeid shrimp fishery. North American Journal of Fisheries Management 28:1828–1842.

Gitschlag, G. R., M. J. Schirripa, and J. E. Powers. 2003. Impacts of red snapper mortality associated with the explosive removal of oil and gas structures on stock assessments of red snapper in the Gulf of Mexico. *In* Fisheries, reefs, and offshore development, Stanley, D. R., and A. Scarborough-Bull, Editors. American Fisheries Society, Symposium 36:83–94.

Goodyear, C. P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. NMFS-SEFSC Contribution: MIA-94/94-63. Miami, Florida.

Heupel, M. R., and C. A. Simpfendorfer. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal of Fisheries and Aquatic Sciences 59:624–632.

Heupel, M. R., K. L. Reiss, B. G. Yeiser, and C. A. Simpfendorfer. 2008. Effects of biofouling on performance of moored data logging acoustic receivers. Limnology and Oceanography: Methods 6:327–335.

Hightower, J. E., J. R. Jackson, K. H. Pollock. 2001. Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. Transactions of the American Fisheries Society 130:557–567.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 82:898–903.

Hood, P. B., A. J. Strelcheck, and P. Steele. 2007. A history of red snapper management in the Gulf of Mexico. Pages 267–284 *in* W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society Symposium, 60, Bethesda, Maryland.

Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53:820–822.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Manooch III, C. S., J. C. Potts, D. S. Vaughan, and M. L. Burton. 1998. Population assessment of the red snapper from the southeastern United States. Fisheries Research 38:19–32.

Minton, R. V., and S. R. Heath. 1998. Alabama's artificial reef program: building an oases in the desert. Gulf of Mexico Science 16:105–106.

Moseley, F. N. 1966. Biology of the red snapper, *Lutjanus aya* Block, of the northwestern Gulf of Mexico. Publications of the Institute of Marine Science University of Texas 11:90–101.

Nelson, R. S., and C. S. Manooch III. 1982. Growth and mortality of the red snapper, *Lutjanus campechanus*, in the west-central Atlantic and northern Gulf of Mexico. Transactions of the American Fisheries Society 111:465–475.

Patterson III, W. F., J. C. Watterson, R. L. Shipp, and J. H. Cowan Jr. 2001. Movement of tagged red snapper in the Northern Gulf of Mexico. Transactions of the American Fisheries Society 130:533–545.

Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer 39:175–192.

Peabody, M. B. 2004. The fidelity of red snapper (*Lutjanus campechanus*) to petroleum platforms and artificial reefs in the northern Gulf Of Mexico. Master's Thesis. Louisiana State University, Baton Rouge, Louisiana.

Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 41:1117–1120.

Pine, W. E., K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28:10–23.

Pollock, K. H., H. Jiang, and J. E. Hightower. 2004. Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. Transactions of the American Fisheries Society 133:639–648.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

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

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Rose, K. A., J. H. Cowan Jr, K. O. Winemiller, R. A. Myers, and R. Hillborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293–327.

Schroeder, W. W.,A. W. Shultz, and J. J. Dindo. 1988. Inner-shelf hardbottom areas, northeastern Gulf of Mexico. Gulf Coast Association of Geological Societies Transactions 38: 535–541.

Schroepfer, R. L., and S. T. Szedlmayer. 2006. Estimates of residence and site fidelity for red snapper *Lutjanus campechanus* on artificial reefs in the northeastern Gulf of Mexico. Bulletin of Marine Science 78:93–101.

Schirripa, M. J., and C. M. Legault. 1999. Status of the red snapper in U.S. waters of the Gulf of Mexico: updated through 1998. Southeast Fisheries Science Center, Miami Laboratory, NMFS, SFD-99/00-75.

SEDAR7. 2005. Stock assessment report of SEDAR 7, Gulf of Mexico Red Snapper. NMFS, SEFSC, NOAA, Charleston, South Carolina. Available: http://www.sefsc.noaa.gov.(January 2009).

SEDAR. 2009. Stock Assessment of Red Snapper in the Gulf of Mexico: SEDAR Update Assessment. NMFS, SEFSC, NOAA, Miami, Florida. Available: http://www.sefsc.noaa.gov.(January 2009).

Slipke, J. W., and M. J. Maceina. 2005. Fisheries analyses and simulation tools (FAST 2.1). Auburn University, Auburn, Alabama USA.

Stanley, D. R., and C. A. Wilson. 1989. Utilization of offshore platforms by recreational fishermen and SCUBA divers off the Louisiana coast. Bulletin of Marine Science 44:767–775.

Starr, R. M., V. O'Connell, S. Ralston, L. Breaker. 2005. Use of acoustic tags to estimate natural mortality, spillover, and movements of lingcod (*Ophiodon elongatus*) in a Marine Reserve. Marine Technology Society Journal 39:19–30.

Summerfelt, R. C., and L. S. Smith. 1990. Anesthesia, surgery, and related techniques. In: Schreck, C. B., and P. B. Moyle (eds) Methods for Fishery Biology. Bethesda: American Fisheries Society, 213–272.

Szedlmayer, S. T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial reef sites in the northeast Gulf of Mexico. Copeia 1997:846–850.

Szedlmayer, S. T. 2007. An evaluation of the benefits of artificial habitats for red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute 59:223-229.

Szedlmayer, S. T., and R. L. Schroepfer. 2005. Long-term residence of red snapper on artificial reefs in the northeastern Gulf of Mexico. Transactions of the American Fisheries Society 134:315–325.

Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the Northeastern Gulf of Mexico. Bulletin of Marine Science 55:887–896.

Topping, D. T., and S. T. Szedlmayer. 2011a. Site fidelity, residence time and movements of red snapper *Lutjanus campechanus* estimated with long-term acoustic monitoring. Marine Ecology Progress Series 437: 183–200.

Topping, D. T., and S. T. Szedlmayer. 2011b. Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs. Fisheries Research doi:10.1016/j.fishres.2011.08.013.

Watterson, J. C., W. F. Patterson III, R. L. Shipp, and J. H. Cowan Jr. 1998. Movement of red snapper, *Lutjanus campechanus*, in the north central Gulf of Mexico: potential effects of hurricanes. Gulf of Mexico Science 1998:92–104.

Westmeyer, M. P., C. A. Wilson, and D. L. Nieland. 2007. Fidelity of red snapper to petroleum platforms in the northern Gulf of Mexico. Pages 105–121 *in* W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society Symposium, 60, Bethesda, Maryland.

Wilson, C. A., and D. L. Nieland. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. Fishery Bulletin 99:653–664.

Winter, J. D. 1983. Underwater biotelemetry. Pages 371–395 In: L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Young, S. P., and J. J. Isely. 2004. Temporal and spatial estimates of adult striped bass mortality from telemetry and transmitter return data. North American Journal of Fisheries Management 24:1112–1119.

Table 1. Summary of release information (total length, TL; weight, Wt) and number of days (event time) from release until occurrence of the specified event (emigration = E, fishing mortality = F, natural mortality = M, present = P, unknown = U) for ultrasonically-tagged red 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_∞ = 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)	$M = -\log_e(\mathrm{Ps}) / t_{max}$	(0.11)
		0.09
Peterson and Wroblewski (1984)	$M = 1.92(W_{max}^{-0.25})$	0.16
Pauly (1980)	$\log(M) = -0.0066 - 0.279 \log(L_\infty)$	0.36
	$+ 0.6543 \log(K) + 0.4634 \log(T)$	
Chen and Watanabe (1989)	$M = 1 / (\mathrm{inAge} - \mathrm{finAge})$	0.20
	$\cdot \log_e\{[e^{(K\cdot \mathrm{finAge})} - e^{(K\cdot t0)}] / [e^{(K\cdot \mathrm{inAge})} - e^{(K\cdot t0)}]\}$	

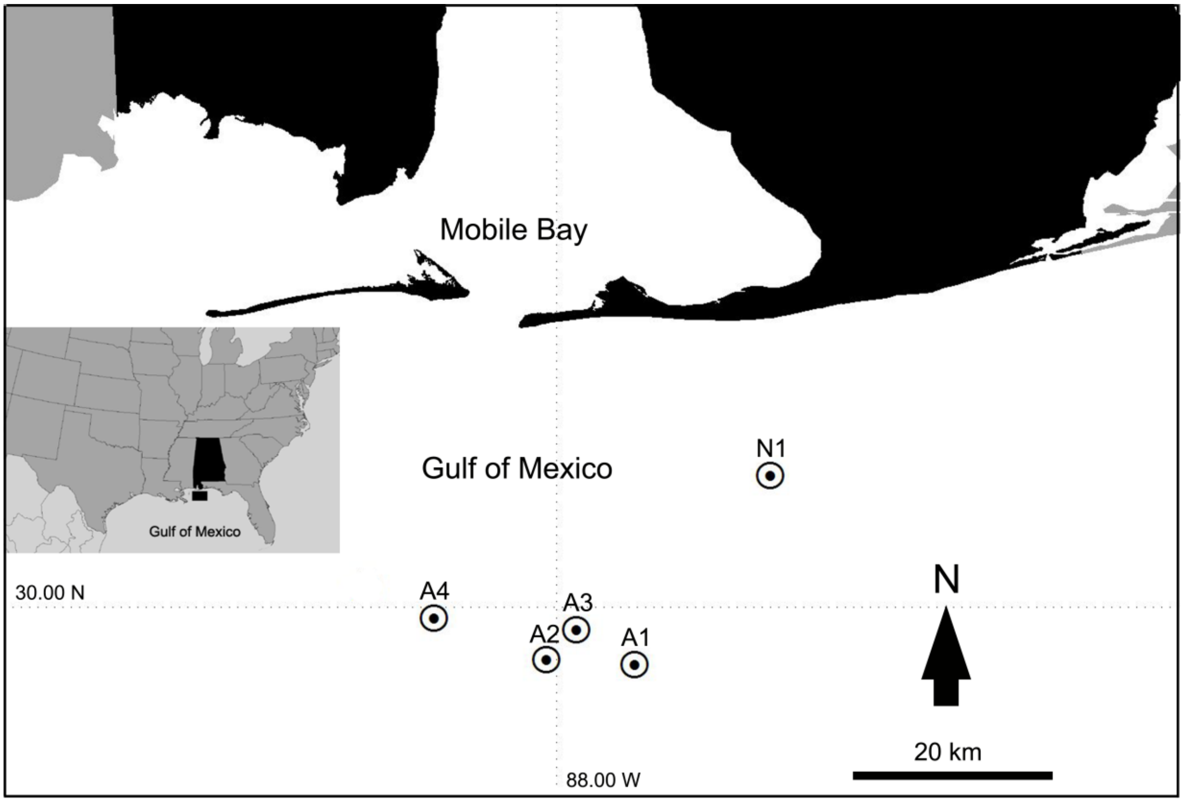

Figure 1. Location of study sites (A1–A4, N1) in the northeast Gulf of Mexico. Inset (middle left) shows Gulf of Mexico and study area (black box) offshore Alabama (black), USA.

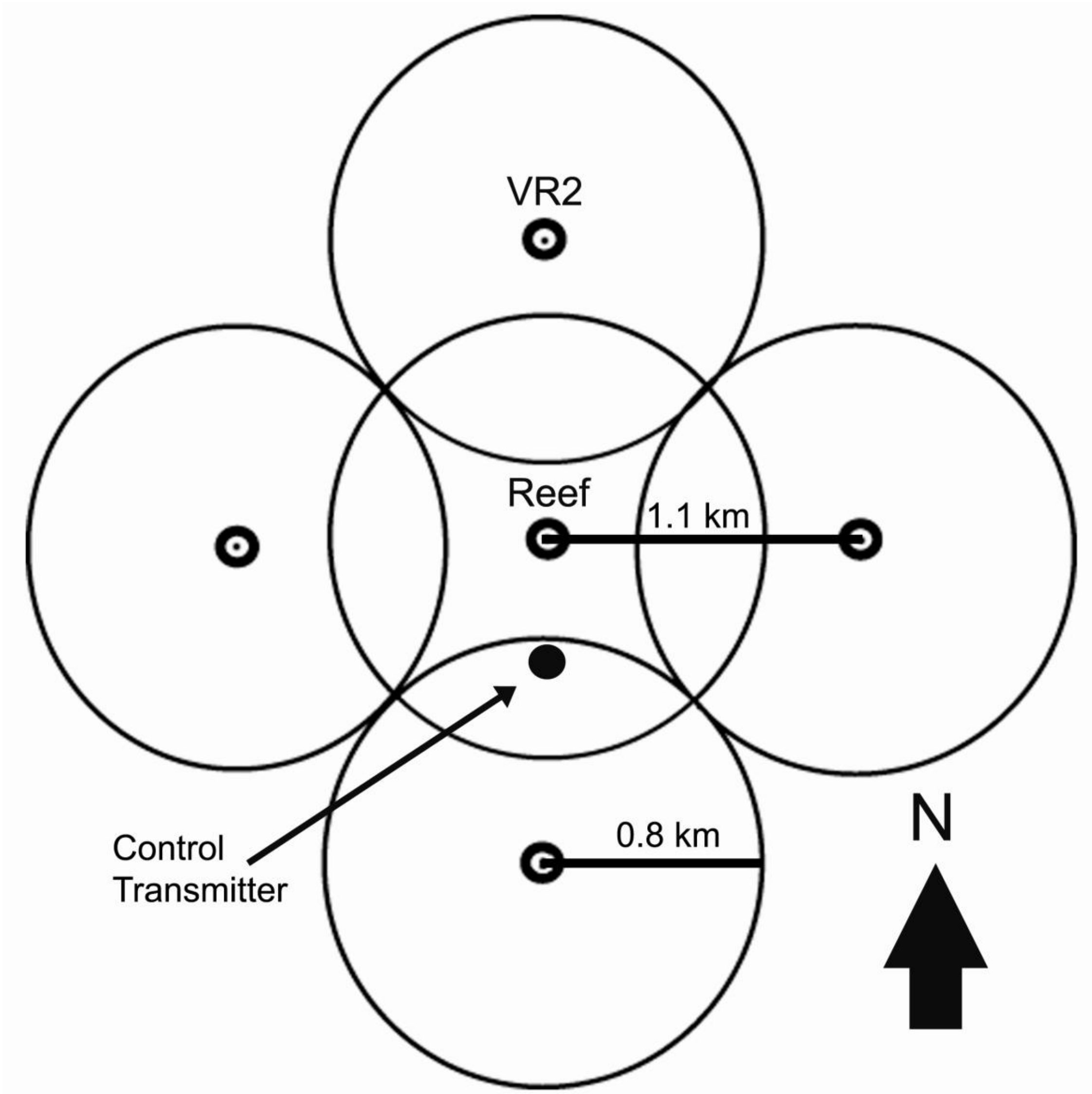

Figure 2. Receiver array design for each site, with one receiver at the reef and four others surrounding the reef 1.1 km (0.4 km at site A4) away to the N, S, E, and W. Circles represent detection range of 0.8 km. A stationary control transmitter was placed 400 m S of reef (150 m at A4).

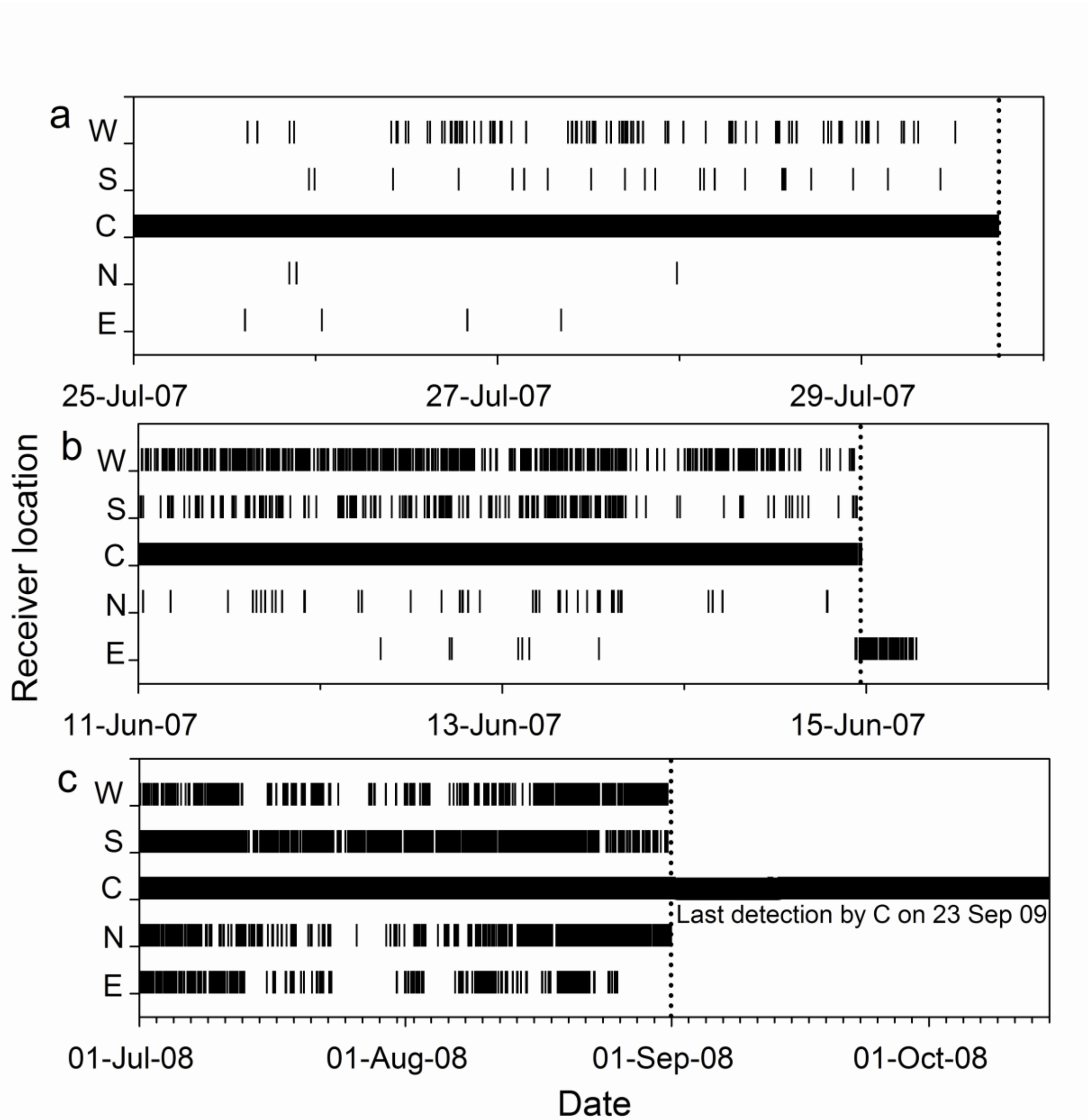

Figure 3. Plots showing examples of the detection patterns expected from fish experiencing either a) fishing mortality, b) emigration, or c) natural mortality events. Each plot shows a segment of the overall detections of a single fish by the Center (C), North (N), South (S), East (E), and West (W) receivers at its site of release. The vertical dashed lines indicate the occurrence of the specified event. Note: different scales for X-axis.

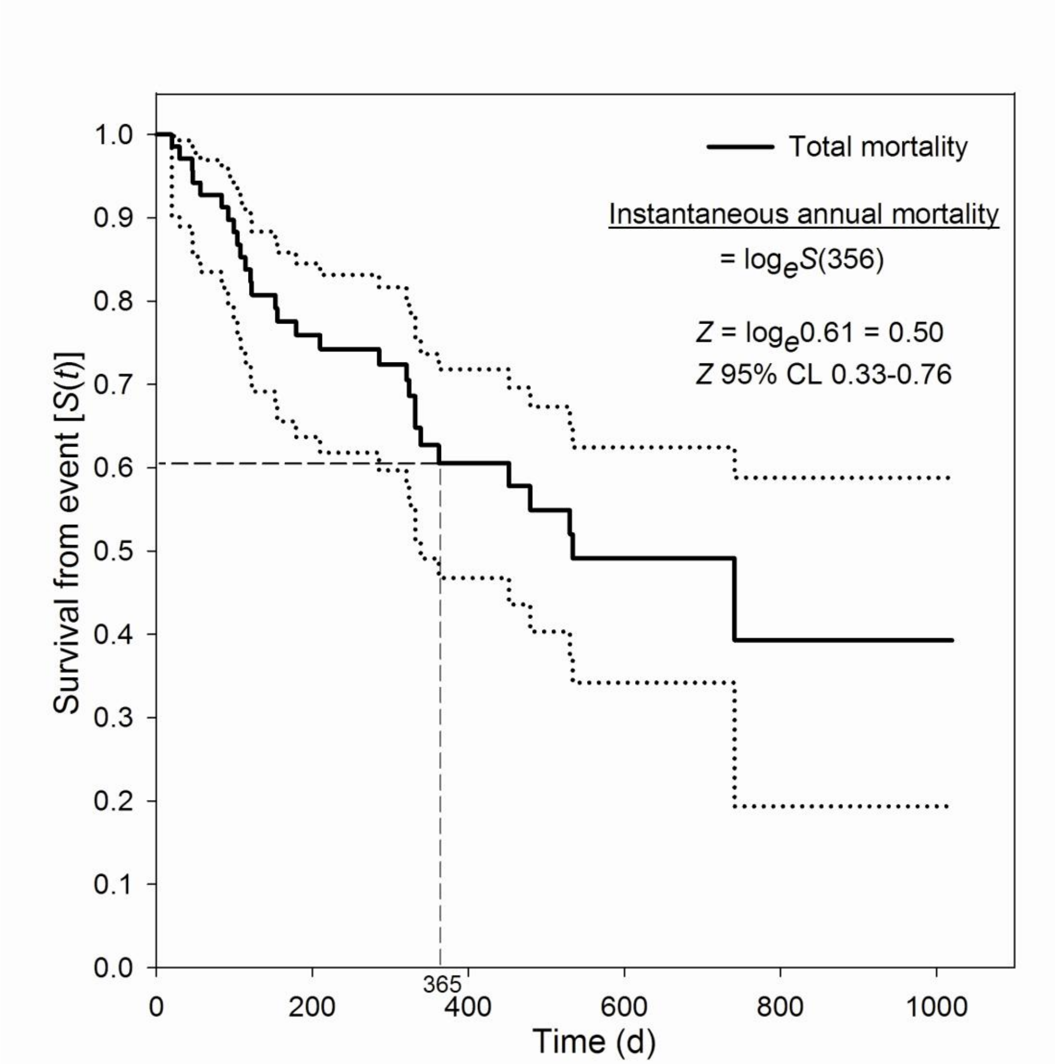

Figure 4. Kaplan-Meier (K-M) estimation of survival (S_Z) of red snapper from total mortality (fishing and natural mortality). Dashed lines show proportion of fish (61%) surviving total mortality at 365 d (*t*). Dotted lines are 95% confidence limits (CL). Instantaneous total mortality (*Z*) is calculated from proportion surviving at 365 d and *Z* 95% CL is calculated from survival at 365 d at 95% CL.

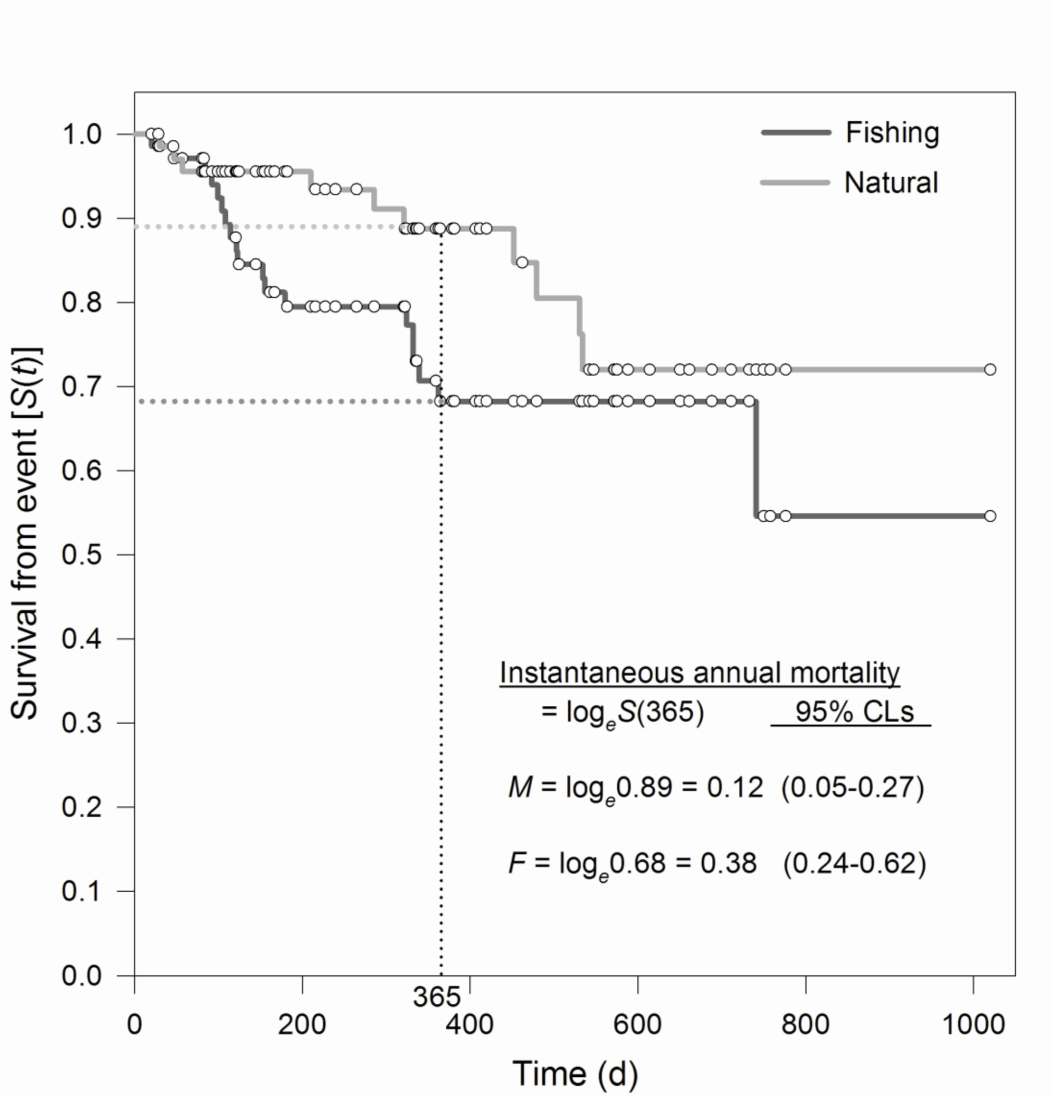

Figure 5. Kaplan-Meier (K-M) estimation of survival (*S*) of red snapper from fishing (dark gray) and natural mortality (gray). Dashed lines show proportion of fish surviving fishing and natural mortality at 365 d (*t*). Instantaneous fishing (*F*) and natural (*M*) mortality rates calculated from proportion surviving each mortality at 365 d and 95% CL is calculated from 95% confidence limits of *S*(365) for each survival probability (not shown).

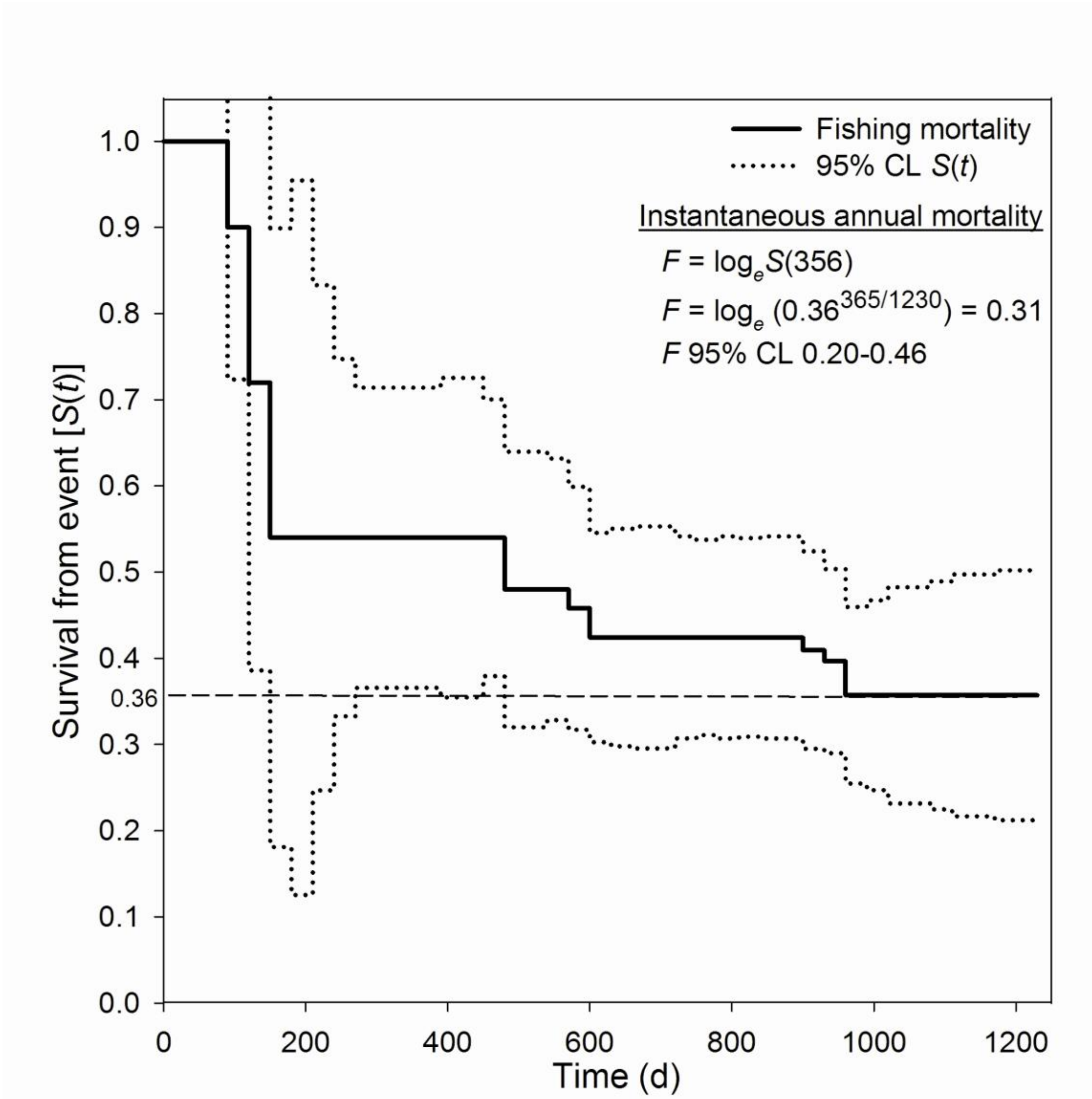

Figure 6. Staggered entry estimation of survival (S) of red snapper from fishing mortality. Dashed line shows proportion (36%) of fish surviving fishing at 1230 d (t). Instantaneous fishing (F) mortality rates calculated from proportion surviving at 1230 d, adjusted to $S_F(365) = 74\%$. Dotted lines are 95% confidence limits (CL). Day 0 is 13 December 2005.

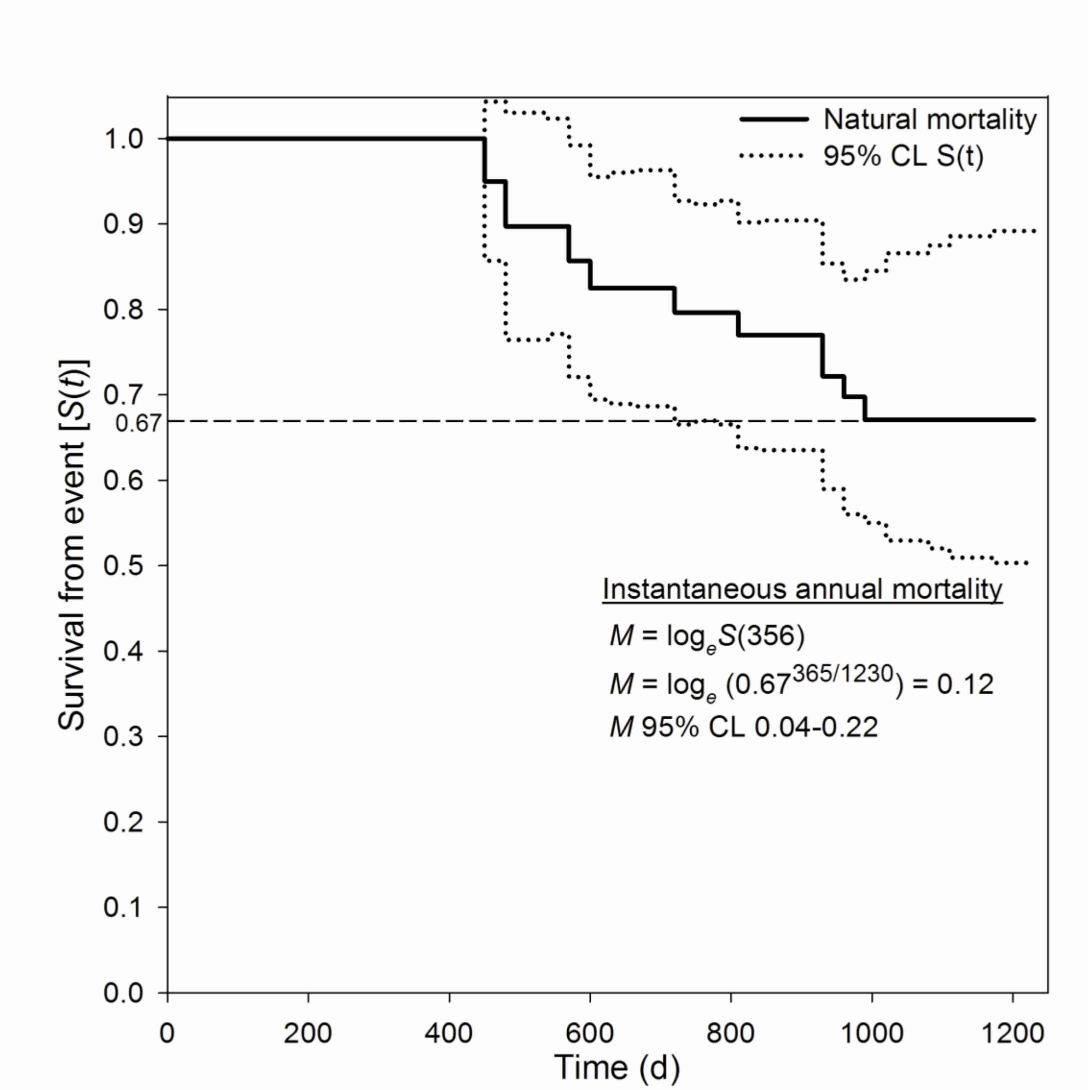

Figure 7. Staggered entry estimation of survival (*S*) of red snapper from natural mortality. Dashed line shows proportion (67%) of fish surviving natural mortality at 1230 d (*t*). Instantaneous natural (*M*) mortality rates calculated from proportion surviving at 1230 d, adjusted to $S_M(365) = 89\%$. Dotted lines are 95% confidence limits (CL). Day 0 is 13 December 2005.

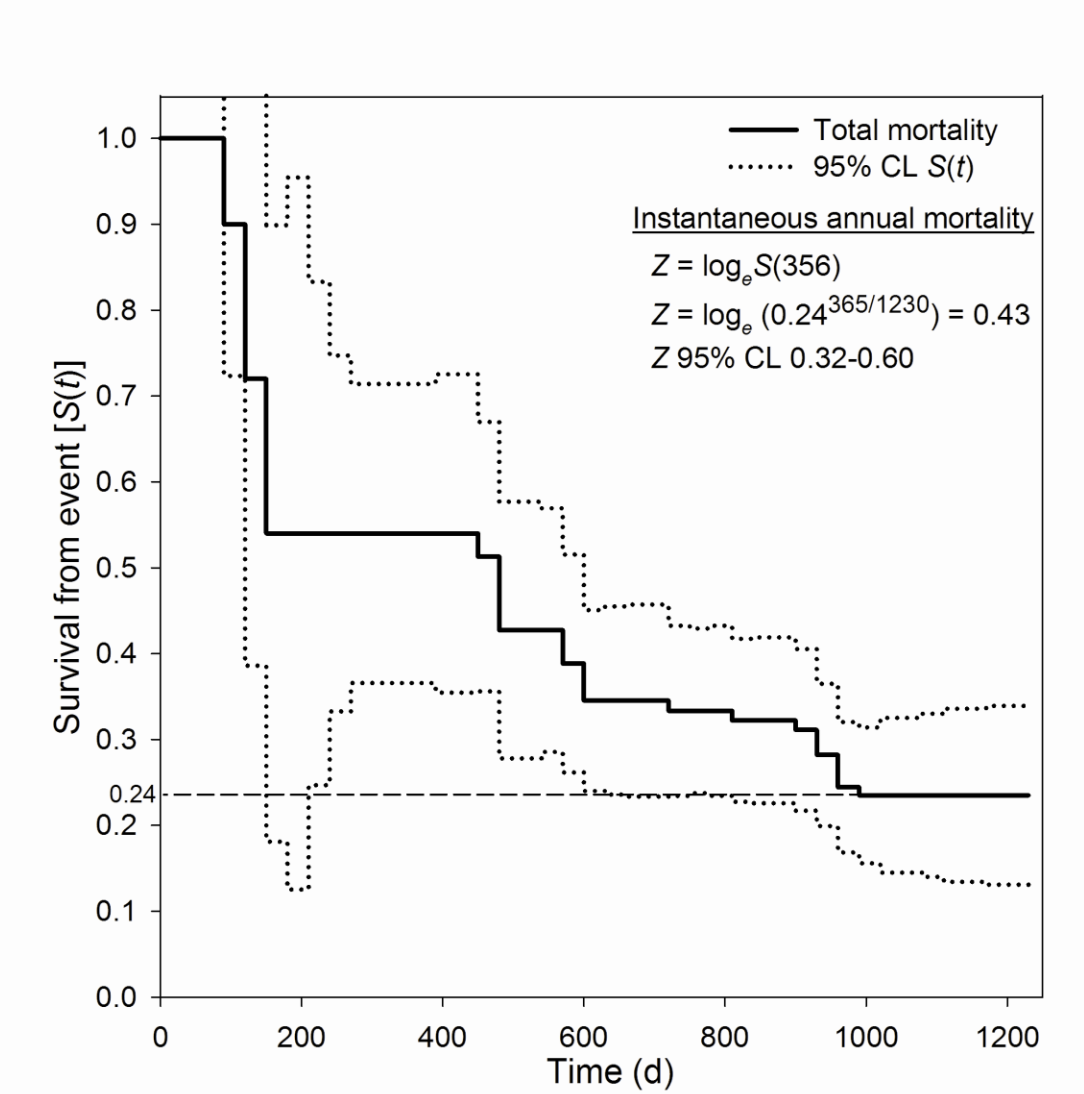

Figure 8. Staggered entry estimation of survival (*S*) of red snapper from total mortality (fishing and natural). Dashed line shows proportion (24%) of fish surviving total mortality at 1230 d (*t*). Instantaneous total (*Z*) mortality rates calculated from proportion surviving at 1230 d, adjusted to $S_Z(365) = 65\%$. Dotted lines are 95% confidence limits (CL). Day 0 is 13 December 2005.