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[Article]

Age Composition, Growth, and Density-Dependent Mortality in Juvenile Red Snapper Estimated from Observer Data from the Gulf of Mexico Penaeid Shrimp Fishery

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Abstract.—Beginning in May 1998, the National Marine Fisheries Service has required that bycatch reduction devices be installed in penaeid shrimp trawl gear in the Gulf of Mexico. Changes in observer protocols were introduced, one of which was that all of the red snapper *Lutjanus campechanus* collected would be enumerated and measured when possible. This change has yielded catch and length information from the Gulf of Mexico shrimp fishery. To date, however, an integrated approach to determining the age composition, growth, and mortality of juvenile red snapper has not been attempted. To address this problem, we constructed a length-based, age-structured model to objectively estimate the growth and mortality parameters and age composition of the shrimp trawl bycatch of red snapper in the western Gulf of Mexico from 81 monthly length frequency data sets (a total of 239,521 fish were measured) from July 1999 to February 2007. Our modeling strategy was to make simple and straightforward representations of the deviations in growth from the mean trend, partial recruitment, density-dependent mortality, and population dynamics. Bayesian parameter estimation was accomplished by calculating the mode of the posterior distribution. Important findings of this paper include (1) the shrimp trawl bycatch during the first and third trimesters is dominated (86–87%) by age-0 fish, (2) the growth patterns of age-0 and age-1 red snapper suggest that the fish form an opaque annulus in winter months, (3) the natural mortality of age-0 fish appears to be about double (a minimum 70% increase) the value used in the last stock assessment, and (4) the evidence for density-dependent juvenile mortality is overwhelming. Inclusion of these findings in the red snapper stock assessment has the potential to substantially alter management practices.

The red snapper *Lutjanus campechanus* supports important recreational and commercial fisheries in the Gulf of Mexico. Juveniles (ages 0 and 1) are also taken as bycatch in the Gulf penaeid shrimp fishery (Goodyear 1994, 1995). The red snapper stock has been overfished since at least 1994, and rebuilding efforts to date have been unsuccessful (SEDAR7 2005). In the mid to late 1990s, it was determined that if shrimp trawl bycatch mortality could be reduced by 50% or more, the stock would rebuild and support a total allowable catch (TAC) of 4.14 million kg in the directed fisheries (Goodyear 1995; Schirripa and Legault 1997). A major component of the rebuilding strategy was the belief that certain bycatch reduction devices, or BRDs, developed and tested during the early to mid-1990s, would reduce bycatch mortality by about 60% (Watson et al. 1997). In contrast, Gallaway and Cole (1999) suggested that the maximum theoretical reduction that could be achieved using these devices would be on the order of 25–27%, and the actual reduction would likely be much less.

The National Marine Fisheries Service (NMFS) required that BRDs be installed in penaeid shrimp trawl gear in the gulf beginning in May 1998 (Gallaway and Cole 1999). Coincident with the new BRD requirement, the observer program for the gulf shrimp fishery focused on gathering additional data that would improve estimates of BRD effectiveness as well as the magnitude and size composition of the red snapper bycatch. Changes in observer protocols were introduced, one change being that all red snapper collected would be enumerated and measured where possible. This change has yielded a wealth of red snapper catch and length information for most years since 1998.

The SEDAR7 (2005) stock assessment determined that red snapper remained overfished, mainly because

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(1) the BRDs had failed to achieve the target mortality reduction and (2) the TAC had been maintained throughout the 1998–2003 period at a level that assumed the bycatch mortality reduction was being met. Bycatch estimates (Nichols 2005a, 2005b) were improved by both the new red snapper observer data and by the development of an improved bycatch model. The red snapper length data gathered by observers were used to make subjective estimates of the age-0 and age-1 fractions in the bycatch (Nichols 2005c). Nichols et al. (2005) also used seasonal scientific survey data (Southeast Area Mapping and Assessment Program [SEAMAP]) describing size–age distributions, abundance, and effort data to estimate that the instantaneous natural mortality (M) was 0.6 for age-1 red snapper. This value was used in conjunction with the ratio of age-0 to age-1 mortality used by Goodyear (1995) to infer that M for age-0 red snapper was 1.0 (SEDAR7 2005). These values were used in the SEDAR7 (2005) assessment as the best estimates of M for age-0 and age-1 red snapper.

Other M values for juvenile red snapper were also considered but not adopted. For example, Szedlmayer et al. (2005) estimated that total mortality for age-0 fish in an untrawled habitat was 2.3, and he suggested that age-0 M was about 2.0. In addition, the Assessment Workshop group of SEDAR7 (Southeast Data, Assessment, and Review: Gulf of Mexico Red Snapper) believed that there was evidence that natural mortality for juvenile red snapper was density dependent (e.g., see Gazey 2005; McAllister 2005a, 2005b; Powers and Brooks 2005). This evidence was summarized in Section 3 of SEDAR7 (2005) and, more recently, Gallaway et al. (in press) has provided additional evidence supporting the concept of density-dependent mortality for juvenile red snapper. The Assessment Workshop of SEDAR7 attempted to approximate the effects of density-dependent mortality by simply not including age-0 bycatch in the assessment. This approach, which assumes bycatch mortality of age-0 fish was insignificant compared with natural mortality, was rejected by the subsequent SEDAR7 Review Workshop. However, Cordue (2005) recommended that future red snapper stock assessments should model postrecruitment density-dependent mortality "as this is critical for determining the impact of penaeid shrimp trawl bycatch on red snapper rebuilding."

An integrated approach for dealing with the age composition, growth, and mortality of juvenile red snapper has not been previously attempted. Modern application of length frequency information to population dynamic statistical models has been pioneered by Fournier et al. (1990, 1998). The post-1998 observer data from the Gulf of Mexico penaeid shrimp fishery provided information on juvenile red snapper length and catch that enabled us to construct a length-based, age-structured model patterned after the approaches developed by Fournier and colleagues. This model was used to objectively estimate growth and mortality parameters, and the age composition of the shrimp trawl bycatch of red snapper from multiple length frequency data sets. Our specific objectives in modeling these data were to (1) estimate the age composition of the bycatch by year and trimester, (2) describe monthly or seasonal growth deviations from the mean trend, (3) estimate total apparent mortality, and (4) evaluate the inferential evidence for density-dependent mortality.

Methods

Length frequency, catch, and effort observations.— The length frequency observations used in this analysis came from the NMFS's post-1998 Observer File, a database housed at the Galveston Laboratory of the Southeast Fisheries Science Center. A history and description of the Gulf of Mexico and Southeast Atlantic Shrimp Trawl Observer Program is provided by Scott-Denton (2005). The projects included in the file that we obtained were coded as follows: B = BRD evaluation; E = effort; G = BRD certification, Gulf of Mexico; M = modified bycatch characterization; R = red snapper initiative; and T = turtle excluder device, or TED, evaluation. In the Gulf of Mexico, most of the data collected from 1999 to the present came largely from the R, E, G, and T studies. Scott-Denton (2005) describes the at-sea data collection methods for these studies.

We restricted our analyses to samples taken in the western Gulf of Mexico (NMFS Statistical Areas 13–21) following the SEDAR7 (2005) red snapper stock assessment. We used red snapper length and catch data and the effort data from all nets on each tow that had a positive value for penaeid shrimp catch recorded in the station sheet form (i.e., a positive shrimp catch was used to indicate an acceptable tow). In some studies (e.g., G and R) data from only two of the four nets were sampled, and the BRD in one of the paired nets was disabled as a basis for evaluating BRD performance. We used data from these nets as well because (1) we wished to use as much of the red snapper length information as possible and (2) the bias resulting from using data from a net in which the BRD had been disabled was believed to be relatively small because of the poor performance of BRDs to date (Foster 2005).

The raw length frequency data for red snapper were placed in 5-mm length bins and summed across all tows for each month and year for the period from July 1999 through February 2007. The programs differed in the number of nets sampled for red snapper count and length information. For example, the E program generally counted and measured all red snapper taken in all nets, usually four. In contrast, red snapper data from only the two outer nets were typically used in programs such as the G, R, and T studies. Whereas we did not believe this was a problem with respect to the length frequency data, a standardization protocol was believed necessary for estimating catch and effort used for calculating abundance indices.

Based on Gallaway et al. (1999), we used red snapper catch and effort data for depths greater than 18.2 m as the basis for determining abundance in the western gulf. For each tow, catch was calculated as catch per net times the number of nets towed. The catches from all tows were then summed to obtain the total catch for each year–month combination. Effort (hours towed) for all observed tows, including tows without red snapper, was summed for the corresponding year–month combinations.

Model definition.—Length frequency samples have a monthly resolution and are ordered by date (i.e., sample $i+1$ was taken directly after sample i). Because age-0 red snapper become available to the penaeid shrimp fishery starting in July, for notational convenience, we reference July as sampling month 1. Consequently, the sampling and biological year occurs over the period July to the following June. Each sample i has an associated sampling month, $m(i)$, and year, $y(i)$. The notation used to describe the model presented below is summarized in Table 1. The variables are organized into indices, data and associated descriptors (any combinations of same), fundamental parameters to be estimated, logged probability density functions, and interim variables (some combination of data and fundamental parameters) used to clarify model description or of interest to the user.

The purpose of this section is to describe the methods used to predict the probability of a fish's belonging to a length interval based on the fundamental parameters to be estimated. The main assumptions are as follows: (1) total mortality is either a function of recruitment (density dependent) or constant over the study (see equations 1a and 1b); (2) the length frequency data consist of only age-0 and age-1 red snapper (see equations 1–5); (3) red snapper are vulnerable to the penaeid shrimp fishery for a maximum of 24 months (see equation 2); (4) the trend in growth over the age-0 and age-1 red snapper cohorts is either linear or tracks a von Bertalanffy curve (see equations 3a and 3b); (5) red snapper are not fully recruited to the shrimp trawl bycatch fishery until October (although there is partial recruitment from July to September; see equation 4); and (6) the lengths of red snapper in each age-class are normally distributed around their mean length (see equation 5).

Total instantaneous mortality for age a and sampling year $y(i)$, $Z_{ay(i)}$, is calculated as a function of the logarithmic deviation in recruitment ($\Delta R_{y(i)}$):

$$Z_{ay(i)} = Z_a \cdot \exp\left\{\delta\left[\Delta R_{y(i)} - \frac{1}{Y}\sum_{y=1}^{Y}\Delta R_y\right]\right\}, \quad (1a)$$

where Y is the number of years sampled. If $\delta = 0$,

$$Z_{ay(i)} = Z_a. \quad (1b)$$

The mean recruitment deviation was subtracted to ensure that a 0 value in recruitment reflects the mean and results in a mortality of Z_a. The impact of recruitment deviation is scaled by the coefficient of density dependence, δ. For $\delta > 0$ mortality increases with recruitment, and for $\delta < 0$ mortality decreases with recruitment. If $\delta = 0$, $Z_{ay(i)} = Z_a$ for any year or recruitment and total mortality is said to be density independent. More complex and biologically relevant characterizations of density dependence are feasible; however, we desired a parsimonious model to enhance inferential power.

The relative abundance dynamics in log-space sequenced through the samples (from $i = 1$ to I) are as follows:

$$N_{01} = \Delta R_1 \quad (2a)$$

$$N_{11} = N_{01} - Z_0 \quad (2b)$$

$$N_{0,i+1} = \Delta R_{y(i+1)} \qquad \text{when } y(i+1) \neq y(i) \quad (2c)$$

$$N_{1,i+1} = N_{0i} - t_i Z_{0y(i)} \qquad \text{when } y(i+1) \neq y(i) \quad (2d)$$

$$N_{a,i+1} = N_{ai} - t_i Z_{ay(i)} \qquad \text{when } y(i+1) = y(i). \quad (2e)$$

At the time of the first sample, equation (2a) seeds the abundance for age-0 fish (N_{01}) to the recruitment deviation (ΔR_1), and equation (2b) seeds age 1 by depleting that abundance by the age-0 mean mortality (Z_0; recruitment measures and the associated mortality are not available prior to the first sample). In subsequent samples, when a new sample year is encountered (July each year), age-0 abundance is set to the associated recruitment deviation (equation 2c), and age-1 abundance is set by depleting the age-0 abundance from the previous sample for the period between samples (equation 2d). When the samples occur during the same sample year, the abundance for both age-classes is depleted by the mortality rate associated with the sample year over the intervening period between samples (equation 2e).

TABLE 1.—Notation used in the length-based, age-structured model developed to estimate juvenile red snapper age composition, growth, and mortality.

Variable	Definition
	Indices
a	Age (a = 0, 1)
h	Cohort age (months, h = 1, 2, . . ., 24)
i	Length frequency sample (i = 1, 2, . . ., I)
j	Length interval (j = 1, 2, . . ., J)
	Data variables
b_U	Penalty weight (default = 1.0) for the logged abundance likelihood
$b_{\Delta l}$	Penalty weight (default = 0.05) for the prior length deviation
$b_{\Delta p}$	Penalty weight (default = 1.0) for the prior age deviation
$b_{\Delta R}$	Penalty weight (default = 1.0) for the prior recruitment deviation
C_i	Total sample catch taken at >18.2 m during sample period i
E_i	Effort to obtain sample catch taken at >18.2 m during sample period i
$m(i)$	Sampling month (1 = July, $m(i)$ = 1, 2, . . ., 12)
n_i	Total number of fish measured in sample i
$\tilde{q}_{ij}$	Proportion in sample i of length interval j
t_i	Time (years) between samples i and i − 1
$\hat{U}_i$	Standardized logarithmic catch per unit-effort for sample i
v_j	Midpoint of length interval j
w	Width of length intervals
$y(i)$	Sampling year (from July to June; $y(i)$ = 1, 2, . . ., Y)
	Fundamental parameters to be estimated
α	Overdispersal coefficient
Δl_h	Seasonal (monthly) length deviation for cohort of age h (24 parameters)
Δp_i	Logarithmic age composition deviation for sample i (I = 81 parameters)
$\Delta R_{y(i)}$	Logarithmic recruitment deviation for year $y(i)$ (Y = 8 parameters)
δ	Coefficient of density dependence
K	von Bertalanffy growth coefficient
λ_h	Recruitment selectivity coefficient for month h (Jul, Aug, or Sep)
μ_a	Mean length of age a (two parameters)
σ_a	SD of length distribution for age a (two parameters)
Z_a	Instantaneous mean total mortality for age a (two parameters)
	Negative log-probability densities
L	Total joint posterior
L_A	Abundance index
L_f	Length frequency
$L_{\Delta l}$	Seasonal length deviation
$L_{\Delta p}$	Age composition deviation
$L_{\Delta R}$	Recruitment deviation
	Interim variables
l_h	Mean length for cohort of age h months (equations 3a and 3b)
N_{ai}	Logarithmic abundance for age-a fish when sample i was collected (equation 2)
p_{ai}	Age-a composition of sample i (equation 4)
q_{ij}	Probability of fish in sample i belonging to length interval j (equation 5)
s_{ai}	Adjustments to age-a composition for partial recruitment and age deviation in sample i (equation 4)
U_i	Standardized logarithmic abundance index for sample i (equation 8)
$Z_{ay(i)}$	Total instantaneous mortality for age a including the impact of density dependence in year $y(i)$ (equations 1a and 1b)

Mean lengths at age (for a cohort of red snapper) take 24 months (at most) to pass through the penaeid shrimp fishery. Because growth was only tracked for this period in this study and fish, in general, display little growth compensation in the first two growing seasons (Ricker 1975:232), we expect little curvature in the growth curve. This suggested a simple linear model, that is,

$$l_h = \mu_0 + (\mu_1 - \mu_0)(h - 1)/12 + \Delta l_h, \tag{3a}$$

where $h = 12a + m(i)$ defines the cohort month as a function of age a and sampling month $m(i)$, and μ_0 and μ_1 are the lengths at the start of age 0 and age 1. The additive length deviation, Δl_h, depicts monthly departures from the length trend, and its characterization was one of the motivations for this study.

An alternative and customary approach is to assume a von Bertalanffy growth curve. As parameterized by Schnute and Fournier (1980), mean length by month h (l_h) is then

$$l_h = \mu_0 + (\mu_1 - \mu_0)\frac{1-\exp[-(h-1)K/12]}{1-\exp(-K)} + \Delta l_h, \tag{3b}$$

where K is the growth coefficient. The amount of curvature is controlled by K (for small K, growth is nearly linear).

The age composition for each sample was adjusted for partial recruitment during July, August, and September. Also, deviations (errors) in age (Δp_i) were included in the computation of the proportion of age-a red snapper in sample i (p_{ai}), that is,

$$p_{ai} = \frac{s_{ai}\exp(N_{ai})}{\sum_a s_{ai}\exp(N_{ai})}, \tag{4}$$

where

$$s_{ai} = \begin{cases} \lambda_{m(i)}\exp(\Delta p_i) & \text{if } a = 0 \text{ and } m(i) \leq 3 \\ \exp(\Delta p_i) & \text{if } a = 0 \text{ and } m(i) > 3 \\ 1 & \text{otherwise,} \end{cases}$$

and where $\lambda_{m(i)}$ are the recruitment selectivity coefficients for July, August, and September.

The lengths of the fish in each age-class are assumed to be normally distributed and, following Fournier et al. (1990), the probability of fish in sample i of belonging to length interval j (q_{ij}) can be approximated by

$$q_{ij} = \frac{w}{\sqrt{2\pi}}\sum_a \frac{p_{ai}}{\sigma_a}\exp\left\{\frac{-[v_j - l_{12a+m(i)}]^2}{2\sigma_a^2}\right\}, \tag{5}$$

where w is the width of each length interval, σ_a is the standard deviation of the length for age a, and v_j is midpoint of length interval j.

The steps in the calculation of parameters for the model are as follows: (1) calculate Z_{ay} from equation (1a) or (1b) using the fundamental parameters Z_a, δ, and ΔR_y; (2) calculate N_{ai} from equation (2) using Z_{ay} and the fundamental parameter ΔR_y; (3) calculate l_h from equation (3a) or (3b) using the fundamental parameters μ_0, μ_1, K, and Δl_h; (4) calculate p_{ai} from equation (4) using N_{ai} and the fundamental parameters $\lambda_{m(i)}$ and Δp_i; and (5) calculate q_{ij} from equation (5) using p_{ai}, l_h, and the fundamental parameters σ_0 and σ_1.

Model objective function.—The objective of the analysis is to minimize the sum of the negative log-probability density functions (L). In this model we consider five sources:

$$L = L_f + L_U + L_{\Delta l} + L_{\Delta p} + L_{\Delta R}, \tag{6}$$

where L_f is associated with length frequencies, L_U with abundance indices, $L_{\Delta l}$ with seasonal (monthly) length deviations from the mean trend, $L_{\Delta p}$ with age deviations, and $L_{\Delta R}$ with recruitment deviations. The observed length frequency, catch, and effort data contribute to the objective function (equation 6) through the L_f and L_U likelihoods. All the other sources serve to constrain or condition L_f and L_U. The constraints can be viewed in a Bayesian perspective with $L_{\Delta l}$, $L_{\Delta p}$, and $L_{\Delta R}$ prior normal distributions with 0 mean and known variance and L the posterior.

The length frequencies are assumed to exhibit a multinomial distribution. The formal negative log-likelihood, ignoring constant terms, is expressed as

$$\sum_i \sum_j \tilde{q}_{ij} n_i \log_e(q_{ij}),$$

where n_i is the sample size for each sample i, $\tilde{q}_{ij}$ is the sample proportion in each sample of length interval j and q_{ij} the model predicted proportion in sample i of length interval j via equation (5). Fournier et al. (1990) point out that the performance of this likelihood can degrade because it does not fit real data as well as one would expect with a random sample of size n_i. Their solution is to use robust estimators that account for observations when there is almost no probability of observing such a fish (termed a type I deviation; such an error might occur, for instance, through a mistake in recording or the straying of an age-2+ fish from the reef) and when the frequency observed in a length interval is much higher or lower than it should be given the sample size (termed a type II deviation). The robust multinomial version we used was

$$L_f = \sum_i \sum_j \tilde{q}_{ij}\sqrt{n_i}\log_e\left(\frac{0.01}{J} + q_{ij}\right). \tag{7a}$$

The smallest length interval proportion is set to 0.01/J in equation (7a); thus, the formulation is insensitive to type I deviations. For a multinomial distribution, the variance of observing $\tilde{q}_{ij}$ is equal to $q_{ij}(1 - q_{ij})/n_i$ or the information weight is n_i for a given q_{ij}. Since the square root transform impacts large values more than small values, the use of $\sqrt{n_i}$ in place n_i reduces the sensitivity of type II deviations. In addition, the variance of a real size frequency sample is almost certainly much greater than that of a truly random sample of a given size. Furthermore, unexpected deviations in the length frequency location commonly occur, greatly increasing the variability. The square root transform provides a substantial increase in the variance, and subsequent comparisons of alternative model fits to the data are conservative.

An alternative to the multinomial is an overdispersed Dirichlet-multinomial distribution provided by Kim and Margolin (1992). The negative log-likelihood using the same robust modification used for the multinomial distribution, ignoring constant terms, can be expressed as

$$\begin{aligned} L_f = & \sum_i \log_e \Gamma(\sqrt{n_i} + \alpha) \\ & + \sum_i \sum_j \log_e \Gamma\left[\alpha\left(\frac{0.01}{J} + q_{ij}\right)\right] \\ & - \sum_i \sum_j \log_e \Gamma\left[\alpha\left(\frac{0.01}{J} + q_{ij}\right) + \tilde{q}_{ij}\sqrt{n_i}\right] \\ & - I \log_e \Gamma(\alpha), \end{aligned} \tag{7b}$$

where $\log_e \Gamma(z)$ is the log-gamma function (see Press et al. 1992:214) and α is the overdispersal coefficient. As α becomes large, the overdispersed Dirichlet-multinomial distribution found in equation (7b) approaches the multinomial distribution as expressed by equation (7a).

We assumed that the catch per unit effort (CPUE, or C_i/E_i, where the catch and effort observations for sample i are as described above) provided an index of abundance. The logarithmic predicted abundance and the CPUE index were standardized by removing the mean, which yields

$$L_U = b_U \sum_i (U_i - \tilde{U}_i)^2, \tag{8}$$

where

$$\begin{aligned} U_i = & \log_e\left[\sum_a \exp(N_{ai})\right] \\ & - \frac{1}{I}\sum_i \log_e\left[\sum_a \exp(N_{ai})\right], \end{aligned}$$

and

$$\tilde{U}_i = \log_e\left(\frac{C_i}{E_i}\right) - \frac{1}{I}\sum_i \log_e\left(\frac{C_i}{E_i}\right),$$

and b_U is a penalty or weighting factor to be supplied (i.e., not estimated). We assume that the $\tilde{U}$ are distributed normally with 0 mean and known variance V_U; such that

$$V_U = 1/2b_U.$$

Walters and Ludwig (1994) demonstrate that equation (8) is consistent with assuming that the logged proportionality constant (which relates predicted abundance to CPUE) has a prior uniform (noninformative) distribution and can be integrated out of the equation. We set the penalty weight default to 1.0 and thus the variance is 0.5 with a coefficient of variation (CV = SD/mean) of approximately 0.7 (in log-space, SD and CV are approximately equal). In other words, the CPUE index was assumed to be imprecise.

The contribution to the objective function from the length deviations is given by

$$L_{\Delta l} = b_{\Delta l}\sum_h \Delta l_h^2 + b_{\Delta l}\sum_{h=1}^{22}(\Delta l_h - 2\Delta l_{h+1} + \Delta l_{h+2})^2, \tag{9}$$

where the penalty factor $b_{\Delta l}$ governs the variance of the normally distributed prior modified by the second term, which provides smoothing. We set the penalty default weight to 0.05, which provides for a variance of 10 mm.

The contribution to the objective function from the age deviations is given by

$$L_{\Delta p} = b_{\Delta p}\sum_i \Delta p_i^2, \tag{10}$$

and the contribution to the objective function from the recruitment deviations is given by

$$L_{\Delta R} = b_{\Delta R}\sum_y \Delta R_y^2. \tag{11}$$

We set default penalty weights $b_{\Delta p}$ and $b_{\Delta R}$ both to 1.0, which provide a prior CV of approximately 0.7.

Parameter estimation and model inference.—Parameter estimation can be accomplished through calculating the mode of the posterior distribution. Bard (1974) showed that this is equivalent to finding the minimum of the negative log-likelihood functions plus the negative log-probability density functions of the associated priors (i.e., finding the fundamental parameter values that minimize equation 6).

The model definition and minimization of the model objective function were implemented through the software package AD Model Builder (Otter Research Limited 2000). The package allows for the restriction or bounding of parameter values, stepwise optimization and report production of SEs, marginal posterior profiles, and correlation between parameter estimates. AD Model Builder approximates the covariance matrix for parameter estimates with the inverse of the second partial derivatives of the objective function. All SEs cited here were generated by the AD Model Builder software unless otherwise stated.

Goodness-of-fit procedures do not work very well with real length frequency data because of unexpected deviations in the size frequency distribution from one sampling month to the next. An approximate diagnostic check is that the residual (predicted minus observed count) variance, weighted by the square root of the sample size, should be proportional to the sample size to be consistent with the robust multinomial distribution (equation 7a). Consequently, the residual raw and weighted variances were calculated for each sampling month and compared. The residuals were also examined for trends over length and date.

The sensitivity of the parameter estimates to using alternative default weights b_U, $b_{\Delta l}$, $b_{\Delta p}$, and $b_{\Delta R}$ (equations 8–11) multiplied by 0.25–4.0 was explored. Normal probability plots were conducted on the standardized logged abundance residuals, length deviations, age deviations, and recruitment deviations (equations 8–11) to evaluate the normal distribution assumptions.

Fournier et al. (1998) recommend that model inference from alternative model structures (e.g., model comparison of density-dependent and independent mortality assumptions) employ Bayes posterior factors (BPF; Aitkin 1991). The BPF for model 2 over (likelihood of having a better fit to the data than) model 1 is

$$\mathrm{BPF}_{21} = \exp\left[L_1 + L_2 + (P_1 - P_2)\frac{\log_e(2)}{2}\right], \quad (12)$$

where L_1 and L_2 are the negative log-probability posterior density functions and P_1 and P_2 are the number of parameters. Alternatively, Burnham and Anderson (2002) recommend the use of the Akaike information factor (AIF). The AIF for model 2 over model 1 (ignoring lack of fit and effective sample size corrections and after algebraic manipulation) is

$$\mathrm{AIF}_{21} = \exp[L_1 - L_2 + (P_1 - P_2)]. \quad (13)$$

Both approaches have very similar computations; however, BPF_{21} has a smaller penalty (benefit) for the use of more (fewer) parameters. Aitkin (1991) and Burnham and Anderson (2002) use similar terminology for the interpretation of factor values; namely, 0.01–0.05 provides "strong," 0.001–0.01 provides "very strong," and less than 0.001 provides "overwhelming" evidence (values less than 1.0 imply that model 1 fits the data better than model 2).

Results

Overall, our analyses included data from 7,259 tows made in the western Gulf of Mexico (Figure 1). The largest number of tows came from the red snapper initiative and the effort studies, followed by the BRD certification studies (Table 2). With the exception of 2006 (460 tows), each year was characterized by more than 700 tows, the peak number of tows being recorded in 2002 (1,794). Nearly 19,000 individual nets were sampled (2,142 E tows $\times$ 4 nets/tow + 5,157 other tows $\times$ 2 nets/tow). Of these, approximately 5,000 samples were obtained from nets which had no BRD or a

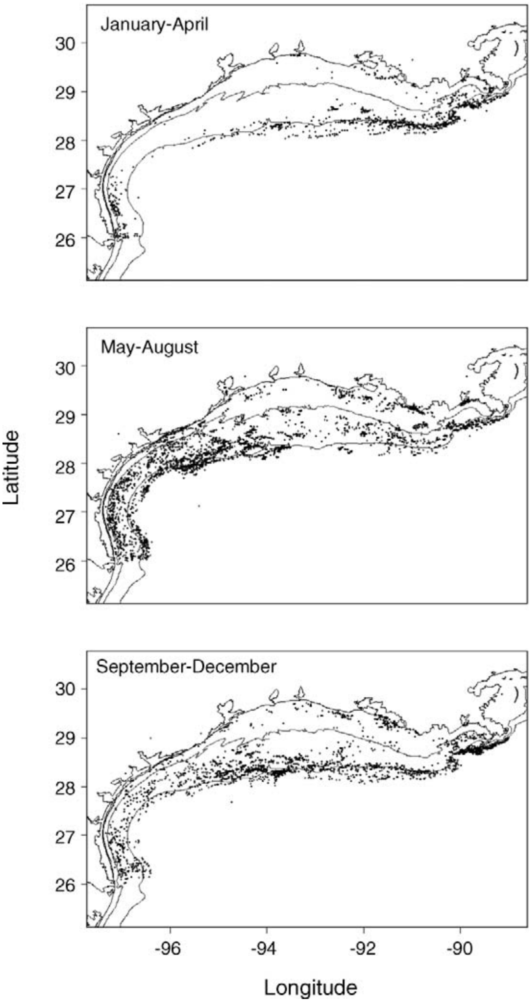

FIGURE 1.—Distribution of observer tows in the penaeid shrimp fishery in the western Gulf of Mexico by trimester, 1999–2005.

TABLE 2.—Number of tows by year and study. Study codes are as follows: B = BRD evaluation, E = effort, G = BRD certification, Gulf of Mexico, M = modified bycatch characterization, R = red snapper initiative, and T = TED evaluation.

Year	B	E	G	M	R	T	Total
1999		449	261				710
2000		475	183			86	744
2001	116	101	211	61	243	43	775
2002	78	643	156	35	709	173	1,794
2003	75	179	179		449	107	989
2004	283		124		505	11	923
2005			258		314	292	864
2006		295	91			74	460
Total	552	2,142	1,463	96	2,220	786	7,259

TABLE 3.—Parameter bounds and initial starting values (see Table 1 for parameter definitions).

Parameter	Bounds		
	Lower	Upper	Initial
Z_0	0.0	20.0	0.3
Z_1	0.0	20.0	0.3
λ_1	0.0	2.0	1.0
λ_2	0.0	2.0	1.0
λ_3	0.0	2.0	1.0
σ_0	10.0	50.0	30.0
σ_1	10.0	50.0	30.0
μ_0	60.0	90.0	75.0
μ_1	140.0	250.0	195.0
δ	−4.0	4.0	3.0
K	0.0	2.0	1.0

disabled BRD. A total of 239,521 juvenile red snapper were measured for length.

Model runs using the overdispersed Dirichlet-multinomial distribution (equation 7b) to compute the length frequency likelihood resulted in the over-dispersal coefficient, α, becoming large and the objective function converging to the value obtained with the multinomial distribution (equation 7a). Therefore, the results of model runs presented below were computed using the multinomial version.

Nonlinear minimization problems with many parameters typically have multiple minima (termed local minima) that are not at the desired overall lowest value (termed the global minimum). Often local minima occur at parameter values that are not biologically credible. A strategy to deal with this problem is to restrict or bound the values of some parameters and try different initial or starting values within these bounds. The bounds and initial parameter values we used are provided in Table 3. All other parameters (length, age composition, and recruitment deviations) were unbounded, with zeros for initial values. In general, the bounds are very broad, and the same minimum was found regardless of alternative initial values. The exception occurred for model runs that applied density-dependent mortality. If the density-dependent mortality coefficient (δ) was started near the lower bound (−4.0), the subsequent estimate for δ was about 0.4. On the other hand, if δ was started near the upper bound (4.0), the subsequent estimate was about 1.8.

TABLE 4.—Correlations between parameter estimates, by model option (parameters are defined in Table 1).

Parameter	Mode	SE	Z_0	Z_1	λ_1	λ_2	λ_3	σ_0	σ_1	μ_0	μ_1	δ or K
Von Bertalanffy growth with density-dependent mortality												
Z_0	2.16	0.256	1.000									
Z_1	1.25	0.280	−0.370	1.000								
λ_1	0.008	0.0033	−0.512	0.285	1.000							
λ_2	0.081	0.0281	−0.539	0.247	0.327	1.000						
λ_3	0.696	0.2309	−0.460	0.148	0.271	0.291	1.000					
σ_0	21.1	0.39	0.020	0.224	0.016	0.009	−0.002	1.000				
σ_1	30.7	1.12	−0.041	−0.188	−0.035	−0.020	−0.002	−0.218	1.000			
μ_0	84.1	2.31	−0.010	0.096	0.017	0.014	0.003	0.101	−0.061	1.000		
μ_1	172.4	1.47	0.026	0.217	0.015	0.004	−0.008	0.308	−0.299	−0.212	1.000	
δ	1.82	0.539	−0.471	0.185	0.236	0.240	0.205	−0.007	0.020	0.004	−0.013	1.000
K	0.21	0.106	0.022	−0.218	−0.032	−0.023	−0.004	−0.196	0.147	−0.691	0.158	−0.007
Linear growth with density-dependent mortality												
Z_0	2.15	0.254	1.000									
Z_1	1.37	0.276	−0.360	1.000								
λ_1	0.008	0.0034	−0.510	0.280	1.000							
λ_2	0.082	0.0285	−0.539	0.242	0.325	1.000						
λ_3	0.698	0.2315	−0.459	0.144	0.270	0.289	1.000					
σ_0	21.3	0.38	0.023	0.185	0.011	0.005	−0.002	1.000				
σ_1	30.4	1.09	−0.040	−0.158	−0.033	−0.018	−0.002	−0.198	1.000			
μ_0	87.4	1.61	0.010	−0.073	−0.007	−0.003	0.000	−0.045	0.033	1.000		
μ_1	171.8	1.42	0.018	0.252	0.021	0.009	−0.007	0.347	−0.301	−0.105	1.000	
δ	1.83	0.548	−0.455	0.184	0.230	0.234	0.199	−0.006	0.017	−0.003	−0.007	1.000
Von Bertalanffy growth with density-independent mortality												
Z_0	1.99	0.256	1.000									
Z_1	1.55	0.309	−0.579	1.000								
λ_1	0.010	0.0044	−0.577	0.357	1.000							
λ_2	0.101	0.0359	−0.604	0.330	0.362	1.000						
λ_3	0.799	0.2723	−0.522	0.232	0.310	0.330	1.000					
σ_0	21.1	0.39	0.012	0.193	0.010	0.004	−0.004	1.000				
σ_1	30.7	1.12	−0.039	−0.156	−0.024	−0.011	0.004	−0.191	1.000			
μ_0	84.2	2.31	−0.015	0.086	0.016	0.013	0.003	0.141	−0.215	1.000		
μ_1	172.4	1.47	0.019	0.183	0.007	−0.002	−0.012	−0.692	0.100	−0.059	1.000	
K	0.20	0.105	0.034	−0.194	−0.029	−0.021	−0.004	0.170	0.304	−0.294	−0.217	1.000

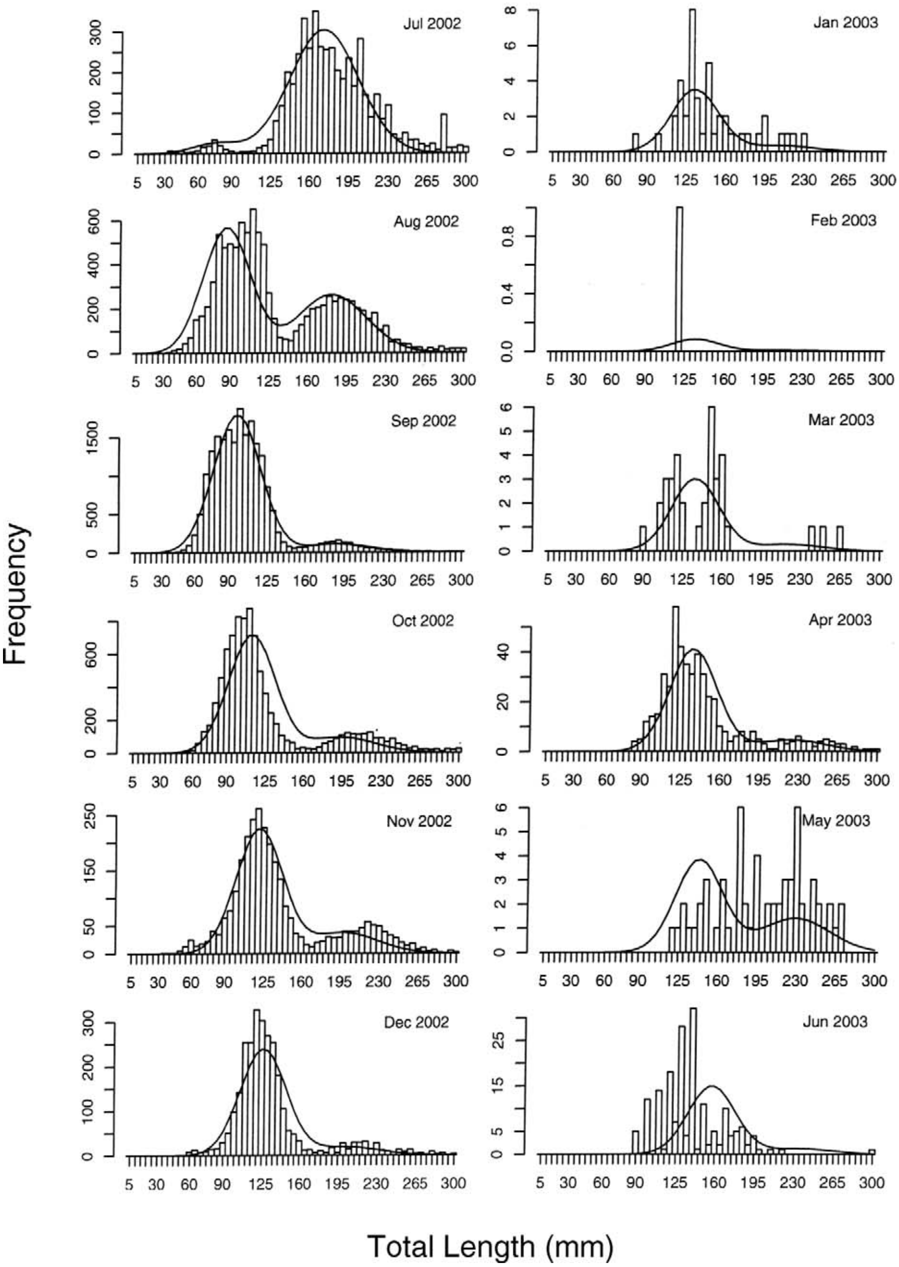

FIGURE 2.—Length frequency data for juvenile red snapper in the western Gulf of Mexico (bars) and the model fit to these data (lines) for the 2002 sample year. The distribution at the smaller lengths in each panel depicts the 2002 year-class.

While both values are in the realm of biological reasonableness, the objective function value for the larger δ was substantially smaller. Therefore, we accepted the conversion at the larger δ and started δ at 3.0 to obtain the global minimum.

Consistent with the robust multinomial distribution, the computed prediction variance of length frequency was quadratic with the sample size and directly proportional to the sample size when the variance was weighted with the square root of the sample size (not shown). Examination of the length frequency residuals over length and date revealed no apparent trends (not shown). Alteration of the penalty weights (equations 8–11) had little impact (<2%) on the

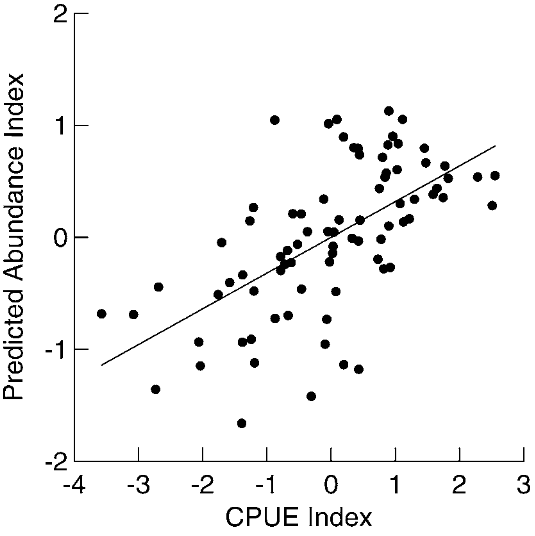

FIGURE 3.—Catch per unit effort index for juvenile red snapper in the western Gulf of Mexico versus the predicted abundance index.

parameter estimates. Consistent with the normal distribution assumptions, the probability plots for the standardized logged abundance residuals, length deviations, age deviations, and recruitment deviations (equations 8–11) were linear (not shown).

Three model options were estimated: (1) von Bertalanffy growth with density-dependent mortality, (2) linear growth with density-dependent mortality, and (3) von Bertalanffy growth with density-independent mortality. Parameter estimates, SEs, and correlations between the parameters for the options are listed in Table 4. A representative display (using model 1) of the length frequency fit for the 2002 sample year is provided in Figure 2, and the fit of the predicted abundance index to the CPUE index can be seen in Figure 3. Model comparisons using the AIF and the BPF are listed in Table 5. Both criteria select model 1 as the best fit to the data. The linear growth option (model 2) is about a third as likely as the model 1, and the density-independent mortality option is less than 1 in 10,000 as likely as model 1.

The estimation results that follow are based on von Bertalanffy growth with density-dependent mortality (model 1). Age composition estimates by calendar year and trimester are listed in Table 6. The first and third trimesters averaged 86–87% age-0 fish, while the age-0 fraction of the bycatch in the second trimester averaged approximately 46%. The monthly mean length and deviation estimates are shown by Figure 4A, and Figure 4B enlarges the deviations from the mean with the associated 2-SE bars. A positive slope indicates growth increments, zero slope an inflection point, and negative slope a cessation in growth. Note that cessation in growth occurs during winter (January–April), and the response to time of year is dampened for age-1 fish.

The standardized (i.e., summing to one) marginal posterior profiles generated by AD Model Builder (Otter Research Limited 2000) for age-0 and age-1 total mean mortality (Z_0 and Z_1) are plotted in Figure 5. According to the profiles, there is a 0.95 probability that Z_0 exceeds 1.69 and that Z_1 exceeds 0.70. Note that the profiles are near normal in shape; thus, inference statements using an SE estimate and normal distribution assumption will be accurate. The standardized marginal posterior profile for the density-dependent mortality coefficient (δ) is plotted in Figure 6. According to the profile, there is a 0.95 probability that δ exceeds 1.28. Note that the shape of the profile is skewed right. This precludes normal approximation for inferential purposes. Age-0 and age-1 density-dependent mortality estimates by year-class (Z_{ay}), as a function of relative recruitment ($\exp[\Delta R_y]$), are plotted in Figure 7 and listed in Table 7.

Discussion

The SEDAR7 (2005) red snapper stock assessment recognized the potential importance of density-dependent mortality but was unable to reach consensus regarding (1) the evidence supporting the timing and magnitude of such a process and (2) how to incorporate this concept into the assessment model. Gallaway et al. (in press) provided a synthesis of the literature describing the life history, distribution, and ecology of the red snapper in the Gulf of Mexico. This information was used to evaluate the evidence for density-dependent mortality and the life stages at which this process might be important. They concluded that the available evidence was consistent with density dependence in survival rate from ages 0–1, and likely

TABLE 5.—Model comparisons using the Akaike information factor (AIF) and posterior Bayes factor (PBF) for inference.

Model	Number of parameters	Function	AIF	BPF
Von Bertalanffy growth with density-dependent mortality	124	12,041.5	1.0000	1.0000
Linear growth with density-dependent mortality	123	12,043.6	0.3329	0.1732
Von Bertalanffy growth with density-independent mortality	123	12,052.4	<0.0001	<0.0001

TABLE 6.—Age composition (percent) of red snapper by year and trimester. Mean ages are weighted by sample sizes (*n*).

	Jan–Apr				May–Aug				Sep–Dec			
Year	Age 0	Age 1	*n*	SE	Age 0	Age 1	*n*	SE	Age 0	Age 1	*n*	SE
1999					87.0	13.0	14,183	2.38	91.4	8.6	26,051	1.72
2000	85.2	14.8	3,695	4.06	68.6	31.4	7,233	4.16	87.8	12.2	32,181	1.96
2001	91.4	8.6	657	4.49	49.9	50.1	9,823	2.84	88.4	11.6	17,457	2.16
2002	80.8	19.2	1,904	4.95	41.9	58.1	15,015	3.58	88.6	11.4	35,443	1.78
2003	86.2	13.8	584	5.54	27.2	72.8	1,974	4.57	85.5	14.5	16,819	2.28
2004	91.6	8.4	4,234	2.34	19.5	80.5	9,559	1.30	59.9	40.1	6,268	3.74
2005	67.8	32.2	979	6.87	10.5	89.5	8,877	1.83	74.6	25.4	8,163	3.27
2006	72.6	27.4	425	7.23	21.2	78.8	5,243	3.75	94.0	6.0	12,323	2.14
2007	90.9	9.1	431	4.57								
Mean	85.5	14.5	12,909	1.71	45.8	54.2	71,907	1.13	87.1	12.9	154,705	0.79

for ages 0–2. However, they did not attempt to quantify the relationships between year-class abundance and mortality based upon literature.

The post-1998 observer program for the gulf penaeid shrimp fishery has generated considerable monthly juvenile red snapper length frequency and catch data from the western Gulf of Mexico that now enable a quantitative assessment of density dependence. Unfortunately, with the exception of the effort study, the vessels carrying observers were not randomly selected. The programs were initially based upon a random sampling protocol, but observer safety, inadequate sleeping facilities, and liability insurance concerns resulted in the initial studies being more of a voluntary charter program than one based on random sampling (Scott-Denton 2005). The problems resulting from the unbalanced sampling have been described by Nichols (2005a, 2005b) and others. Whereas all the observations were taken from representative vessels which were conducting commercial fishing operations, there is no way to evaluate how representative the sample catches are of the monthly population catches. On the positive side, length frequency data should be more robust to unbalanced sampling than other types of data such as catch rate information.

There is also a potential problem associated with our lumping catches from nets with and without BRDs. We

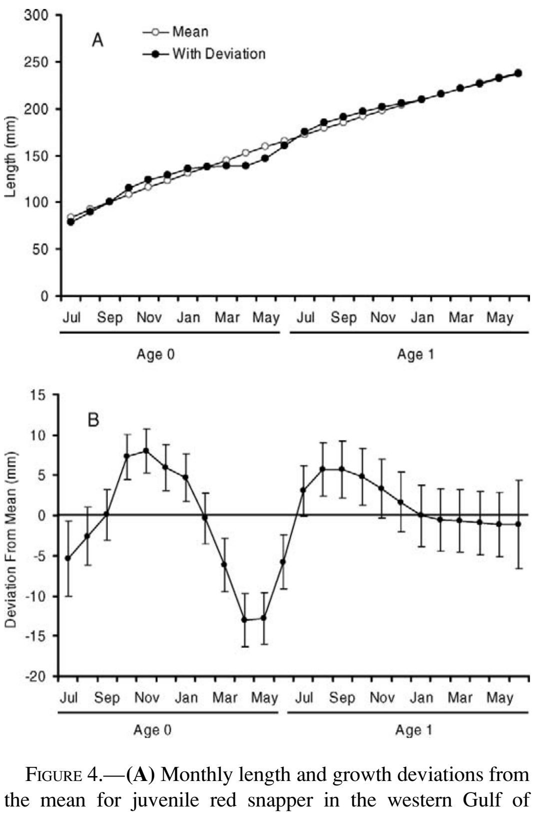

FIGURE 4.—**(A)** Monthly length and growth deviations from the mean for juvenile red snapper in the western Gulf of Mexico and **(B)** an enlarged view of the deviations from the mean.

FIGURE 5.—Standardized marginal posterior profile for juvenile red snapper mean total mortality (Z_0 and Z_1) estimates in the western Gulf of Mexico.

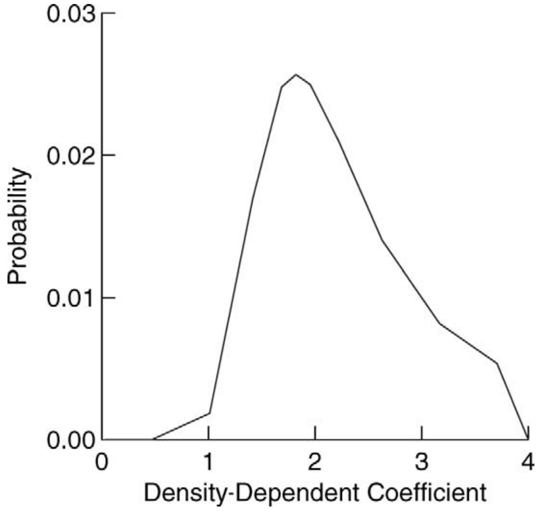

FIGURE 6.—Standardized marginal posterior profile for the density-dependent mortality coefficient (δ) estimate for juvenile red snapper in the western Gulf of Mexico.

believe that this problem is minimal owing to the poor performance of BRDs to date (Foster 2005). Nichols (2005b) noted that he believed the poor performance of BRDs made it unlikely that the imposition of the devices had changed the temporal and spatial distributions of red snapper catches, and that more complex bycatch estimation models incorporating a BRD effect were unnecessary. We concur with this assessment and also with his recommendation urging the development of a stable, comprehensive observer program, as was recommended by the 1997 peer review of the red snapper stock assessment (Nichols 2005b). Collectively, we believe the data analyzed herein represent the

FIGURE 7.—Total mortality of juvenile red snapper in the western Gulf of Mexico as a function of the relative recruitment (Z_{ay}) where the mean recruitment is equal to 1.

TABLE 7.—Recruitment index (mean = 1) and density-dependent mortality by year.

		Total mortality	
Year-class	Recruit index	Age 0 (SE)	Age 1 (SE)
1999	1.151	2.790 (0.883)	1.616 (0.555)
2000	1.040	2.320 (0.721)	1.344 (0.450)
2001	1.140	2.745 (0.861)	1.590 (0.538)
2002	1.218	3.094 (1.072)	1.792 (0.664)
2003	0.532	0.686 (0.277)	0.397 (0.167)
2004	0.772	1.348 (0.545)	0.781 (0.299)
2005	1.192	2.974 (1.018)	1.723 (0.625)
2006	1.230	3.151 (1.286)	1.825 (0.749)

best available data for estimating growth and mortality of juvenile red snapper.

Corrections for lack of fit and effective sample size were not used in the comparison of models. These corrections serve to promote the importance of the difference in the number of model parameters relative to difference in function values for the models under comparison. Since there is only a single parameter difference in each of the comparisons, any impact should be minimal. The application of the square root transform on sample size for the robust multinomial likelihood calculation makes the effective sample size substantially smaller than the number of measured fish. Moreover, the results from using the overdispersed Dirichlet-multinomial distribution to compute the length frequency likelihood indicate that overdispersal is not an important component of the lack of fit. Inspection of the length frequency plots indicates that a major source of lack of fit are unexplained deviations in the size of fish from one sample to the next (e.g., see Figure 2, where October 2002 age-0 fish are smaller than predicted). Our alternative growth and mortality models do not address these deviations, and we expect equal contributions to the overall log-posterior (lack of fit) for these events in the three model comparisons. Overall, comparisons between model options should be conservative and valid.

Our modeling strategy was to make simple and straightforward representations of growth deviations, partial recruitment, density-dependent mortality, and population dynamics. More powerful and biologically relevant approaches may be feasible. For example, a spline function for a piecewise characterization of seasonal growth deviation could be made using fewer parameters than the 24 monthly deviations we used. More complex submodels for density-dependent mortality than the single parameter version we used may be more biologically relevant. While our version (model 1) fit the data better based on AIF, alternative density-dependent parameterizations have approximately equal weight in the data. For example, the comparable AIF was 0.90 when a separate parameter for each age-class was used, and AIF was 0.45 when age-1 density-independent mortality was assumed. In other words, a claim that density-dependent mortality applies only to age-0 juvenile red snapper cannot be rejected with this data. A better understanding of the population dynamics will likely require an expanded model with information on adult age-classes (age 2+), information on juvenile bycatch in the penaeid shrimp fishery, and a larger contrast in recruitment.

The von Bertalanffy growth model with density-dependent mortality (model 1) fit the data somewhat better than the linear growth alternative (model 2). The estimate of the von Bertalanffy growth constant (K = 0.21) compares closely to the value of 0.19 obtained by Patterson et al. (2001) and Wilson and Nieland (2001) using older age-classes. The evidence for the model with density-dependent mortality over the model with density-independent mortality is overwhelming.

The results of our analysis show that the juvenile red snapper bycatch in the gulf penaeid shrimp fishery in the first and third trimesters is dominated by age-0 red snapper (about 86–87%), whereas the catch in trimester 2 (May–August) is split about evenly between age-0 (46%) and age-1 (54%) red snapper (see Table 6). The largest difference in our age composition estimates as compared with existing seasonal estimates (Nichols 2005c) was observed for trimester one. Nichols (2005c) estimated that 99.8% of the juvenile red snapper bycatch during the January–April period consisted of age-1 fish; our estimate was that about 86–87% of the catch during this period was age-0 fish. The reason for this disparity is that Nichols (2005c) promoted all individuals to the next age on 1 January following the Goodyear (1995) convention. As Nichols (2005c) noted, "this is strictly a bookkeeping convention," and that "on January 1, young of the year probably range in true age between 3 and 8 months." Based upon true age, the bycatch of juvenile red snapper in the gulf shrimp fishery is dominated during this period (and overall) by age-0 red snapper.

Based on deviations from monthly mean lengths, a cessation in juvenile red snapper growth occurs between January and April, and the observed seasonal response was less for age-1 than for age-0 red snapper. The January–April period would correspond to the formation of an opaque annulus. Patterson et al. (2001) reported that opaque annulus formation for red snapper occurred during January through May offshore of Alabama. This timing compared to opaque annulus formation during December–June offshore of Louisiana in the western gulf (Wilson and Nieland 2001). Thus, our growth estimates for age-0 and age-1 red snapper are consistent with the premise that, in the Gulf of Mexico, red snapper form one opaque annulus during the winter months and that this is followed by the formation of a translucent annulus during summer (Fischer et al. 2004).

Our recruitment trend for the western gulf for 1999–2006 (see Table 7) followed the trends estimated by Porch (2005) for the years in common. Recruitment was relatively high during 1999–2002, a period followed by a dramatic decline in recruitment in 2003. Our estimates suggested increasing recruitment in 2004 and 2005 as compared with 2003. A similar increase in recruitment for these years is depicted in Figure 7 of Porch (2005).

Our total mortality estimates exceed those reported by SEDAR7 (2005). For age-0 red snapper, mean total mortality for 2001 to 2003 is reported as 1.5 in SEDAR7, whereas our estimate is approximately 2.2 (Table 7). Since natural mortality was a fixed input of 1.0 in SEDAR7 and fishing mortality was estimated to obtain total mortality, the natural mortality must be increased to at least 1.7 or more to obtain consistency between SEDAR7 and this study. For age 1, total mortality for 2001 to 2003 averaged 1.2 in SEDAR7, whereas we estimate a 1.3 mean for 2001 to 2003, approximately. However, our apparent total mortality estimates for age-1 (and possibly age-0) juvenile red snapper include an unknown degree of migration into untrawlable habitat (Gallaway et al., in press).

Important findings of this paper include (1) the penaeid shrimp trawl bycatch during the first and third trimesters is dominated by age-0 juvenile red snapper (86–87%), (2) deviations from the mean growth suggest an opaque annulus is formed during winter months, (3) the natural mortality of age-0 fish appears to be at least 1.7 times higher than the value used in the SEDAR7 (2005) stock assessment, and (4) the evidence for density-dependent juvenile mortality is overwhelming. Inclusion of these findings in the red snapper stock assessment has the potential to substantially alter management practices.

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