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Using demographic analysis to evaluate the potential resilience to exploitation and bycatch and the plausibility of life history parameter values for Gulf of Mexico red snapper (*Lutjanus campechanus*)

April 8, 2004

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Executive Summary

1. Demographic modelling methods were applied to evaluate the resilience implications and plausibility of values assumed for Gulf of Mexico red snapper life history parameters.

2. The parameter values used in the demographic analysis were those in the 1999 stock assessment (Schirripa and Legault 1999) and a range of values for the Beverton-Holt stock recruit function steepness parameter (h) (the fraction of average unfished recruitment when spawning stock biomass is reduced to 20% of unfished conditions) based on estimates for marine demersal species in Myers et al. (1999). The range varied from the mean value for demersal species (Myers et al. 1999), 0.70, to 0.95, the maximum likelihood value in Schirripa and Legault (1999) which is also the maximum of values estimated for marine demersal species (Myers et al. 1999).

3. According to demographic theory, the value for r_m indicates, under average conditions for recruitment, the maximum possible rate of harvest that a population at low abundance can maintain without decreasing in abundance (hr_{max}).

4. The computed values for r_m varied from 0.16 to 0.37 when the value for steepness (h) was increased from 0.70 to 0.95. Thus, the value for r_m depends strongly on the value assumed for h.

5. These values for r_m indicate that *L. campechanus* could have low to moderate resilience to exploitation and that hr_{max}, could range from no higher than 0.37 to 0.16, or lower.

6. By assuming a particular steepness value, and utilizing base case life history parameter values, it is possible to solve for the implied rate of natural mortality for the stage between eggs and age 0 fish (M_{egg}). This should be a very high value, given the very high fecundity of red snapper. The values obtain for M_{egg} were indeed very high. For example, if steepness = 0.90, then M_{egg} = 14.1 yr^{-1}. If steepness was 0.75, then M_{egg} is 15.2yr^{-1}.

7. These extremely high estimates of M_{egg} raise questions over the plausibility of the much lower estimate of age 0 natural mortality rates (M_0) in the 1999 assessment, the period in which age 0 fish are susceptible to bycatch in the shrimp trawl fishery. M_0 was assumed to be only 0.5 yr^{-1} in the 1999 assessment. It is questionable whether this value could be so low relative to the extreme high value for M of 14 yr^{-1} for the stage immediately before it.

8. Further computations were undertaken to evaluate the implications for the current intrinsic rate of increase (r_c) of the current estimates of snapper bycatch mortality in the shrimp trawl fishery and fishing mortality rates from the commercial and recreational fisheries. Using only the estimated 1998 shrimp bycatch mortality estimates and steepness of 0.90, the base case value in NOAA (2003), r_c was 0.22. Using the same steepness and instead only the 1998 commercial and recreational fishing mortality rate estimates, r_c was 0.18. With both sources of mortality included r_c is –0.02 indicating that under average recruitment conditions, the current regime of bycatch and targeting fishing mortality is non-sustainable and may lead to continued decline of the population. With h = 0.95, the r_c from the combined mortalities was positive at 0.04. With lower steepness values, the values for r_c were lower. However, the values for r_c were markedly higher for scenarios with only shrimp bycatch mortality (F_{BC}) than those with only targeted fishing mortality (F_T). In contrast to the 1999 stock assessment, this result indicates that the potential for population increase appears to be impacted more by the recreational and targeted fisheries combined than by the shrimp bycatch fishery.

9. Using h = 0.90, and reducing F_{BC} to 2/3 of the 1998 value but keeping F_T at 1998 levels gives r_c of 0.014 and a population doubling time of 51 years. Reducing F_T to 2/3 of the 1998 value but keeping F_{BC} at 1998 levels gives r_c of 0.033 and a population doubling time of 21 years. Reducing both F_T and F_{BC} to 2/3 of the 1998 levels gives r_c of 0.071 and a population doubling time of 10 years. These results stand in contrast to the findings of the 1999 stock assessment in which reducing shrimp bycatch mortality was instead found to be more important for stock rebuilding than reducing the total allowable catch. In contrast, the demographic results suggest that the potential for stock rebuilding could be enhanced more by reducing the fishing mortality rates from the commercial and recreational fleets than by reducing shrimp bycatch.

Introduction

Demographic analysis (Cortes 1998; McAllister et al. 2001) was carried out for Gulf of Mexico red snapper (*C. campechanus*) using demographic parameters in Schirripa and Legault (1999) and a range of values for the Beverton-Holt stock recruit function steepness parameter (h) (the fraction of average unfished recruitment when spawning stock biomass is reduced to 20% of unfished conditions) based on estimates for marine demersal species in Myers et al. (1999). This was to evaluate the rate of natural mortality from egg to age 0 and maximum and current intrinsic rates of increase implied by the parameters and fishing mortality rate estimates presented in Schirripa and Legault (1999). The impacts of the targeted recreational and commercial and shrimp bycatch fisheries on the realized rate of population increase were thus evaluated. First the demographic method and parameter inputs used are outlined. Second, the demographic results are given. Third, the implications of the results are discussed.

Methods

The maximum intrinsic rate of increase, r_m, was obtained using the following equation:

(1) $$\sum_{x=0}^{A} e^{-r_m x} l_x m_x = 1 \text{ where}$$

A is the assumed age of scenescence.

l_x is computed by:

(2) $$l_x = \prod_{i=0}^{x-1} S_i \ ,$$

where S_i the survial rate at age in the absence of fishing mortality can be expressed as

$S_i = \exp(-M_i)$

where M_i is the instantaenous rate of natural mortality for fish of age i.

m_x the female offspring per female adult at age x can be expressed as a function of the

expected fecundity per individual female, sex ratio s, and the proportion mature ate each age:

(3) $$m_x = s \ g_x f_x$$

where g_x is the expected proportion of individuals mature at age x, and f_x is the fecundity of those mature at age x.

Given that fish over 55 years have appeared in the catches, the assumed age of senescence is 60 years. The rate of natural mortality at age 0 (M_0, for fish from the point from when the first become susceptible to shrimp trawl bycatch to 12 months old) in Schirripa and Legault (1999) is 0.5 yr^{-1}. The assumed rate of natural mortality of age 1 fish is 0.3 yr^{-1}. The assumed rate of natural mortality for ages 2+ years is 0.1. The values for fecundity at age were obtained from Table 1 in Schirripa and Legault (1999) and these values were assumed to reflect the produce of proportion mature at age and fecundity at age. The value for M_{egg}, the rate of natural mortality of eggs to the initial age 0 stage caught by shrimp trawls, was obtained based on the average eggs per recruit (E_0) without fishing, the equation for the Beverton-Holt α parameter and an assumed value for steepness.

$$(4) \qquad \alpha = \frac{E_0(1-h)}{4h}$$

where h is the steepness parameter of the Beverton-Holt stock-recruit function and steepness is defined as the fraction of average unfished recruitment obtained when the spawning stock biomass is reduced to 20% of average unfished conditions. If senescence at age A is assumed, then E_0 is obtained by:

$$(5a) \qquad E_0 = \left(\sum_{i=R}^{A} \exp(iM_{2+}) f_i \right)$$

where A is the age of scenescence (60 years), and R is initial age at maturity (2 years). A second scenario was run in which a plus group at p = 15 years was utlized to evaluate whether this simplication could cause any substantial bias in the results. The formla for E_0 when a plus group is modelled is:

$$(5b) \qquad E_0 = \left(\sum_{i=R}^{p-1} \exp(iM_{2+}) f_i + \frac{\exp\left(-\left(M_{egg} + M_0 + M_1 + (p-1)M_{2+}\right)\right)}{1-\exp(-M_{2+})} f_p \right)$$

With the plus group age, p, set at 15, Equation 1 was still run to age 60 but the values for m_x for ages older than 15 were fixed at the age 15 value to model the effect of assuming a plus group at age 15.

M_{egg} was then computed as follows:

$S_{egg} = 1 / \alpha$

$M_{egg} = - \ln(S_{egg})$

The value of r_m was found by first assuming a particular value for steepness (h), solving for M_{egg}, and then using solver in Excel to find a value for r_m that satisfied equation 1.

Values for the current intrinsic rate of increase (r_c) were obtained by adding the estimated fishing mortality rate at age in 1998 from Table 28, p. 85, Schirripa and Legault (1999) to the natural mortality rate at age. The potential impact of shrimp bycatch on r_c was evaluated by assuming that the entire estimated fishing mortality rate for age 0 and age 1 fish resulted from bycatch. The impact of targeted fishing (recreational and commercial fishing) on r_c was evaluated by assuming that the entire estimated fishing mortality rate from ages two and older resulted from targeted fishing only. The values for steepness (h) that were evaluated included 0.70, 0.75, 0.80, 0.85, 0.90 and 0.95. The values of 0.70, 0.75 and 0.82 are the mean, median and modal (most common) values of steepness values for the 23 marine demersal fish species in Myers et al. (1999). The value of 0.90 is the base case value assumed in NOAA (2003) and the value of 0.95 is maximum likelihood estimate in Schirripa and Legault (1999) and the maximum estimated value from the 23 marine demersal fish species in Myers (1999).

Population doubling time (D) in the absence of density dependence, given r_m or r_c is computed as:

$D = 1 / r_m \ln(2)$.

Results

The computed values for r_m varied from 0.16 to 0.37 when the value for steepness (h) was increased from 0.70 to 0.95 (Table 1). Thus, the value for r_m depends strongly on the value assumed for h.

By assuming a particular steepness value, and utilizing base case life history parameter values, it is possible to solve for the implied rate of natural mortality for the stage between eggs and age 0 fish (M_{egg}). This should be a very high value, given the very high fecundity of red snapper. The values obtain for M_{egg} were indeed very high (Table 1). For example, if steepness = 0.90, then M_{egg} = 14.1 yr^{-1}. If steepness was 0.75, then M_{egg} is 15.2yr^{-1}.

Further computations were undertaken to evaluate the implications for the current intrinsic rate of increase (r_c) of the current estimates of snapper bycatch mortality in the shrimp trawl fishery and fishing mortality rates from the commercial and recreational fisheries. Using only the estimated 1998 shrimp bycatch mortality estimates and steepness of 0.90, the base case value in NOAA (2003), r_c was 0.22 (Table 1). Using the same steepness and instead only the 1998 commercial and recreational fishing mortality rate estimates, r_c was 0.18. With both sources of mortality included r_c is –0.02 indicating that under average recruitment conditions, the current regime of bycatch and targeting fishing mortality is non-sustainable and may lead to continued decline of the population. With h = 0.95, the r_c from the combined mortalities was positive at 0.04 (Table 1). With lower steepness values, the values for r_c were lower. However, the values for r_c were markedly higher for scenarios with only shrimp bycatch mortality (F_{BC}) than those with only targeted fishing mortality (F_T).

Using h = 0.90, and reducing F_{BC} to 2/3 of the 1998 value but keeping F_T at 1998 levels gives r_c of 0.014 and a population doubling time of 51 years (Table 2). Reducing F_T to 2/3 of the 1998 value but keeping F_{BC} at 1998 levels gives r_c of 0.033 and a population doubling time of 21 years. Reducing both F_T and F_{BC} to 2/3 of the 1998 levels gives r_c of 0.071 and a population doubling time of 10 years.

Table 1. Estimates of the natural mortality rate of eggs (M_{egg}), maximum intrinsic rate of increase (r_m), current potential for population increase (r_c) and population doubling time (D) in the absence of density dependent survival and fecundity as a function of Beverton-Holt steepness.

	M_{egg}	r_m	D	r_c	D	r_c	D	r_c	D
steepness				SBC only		TF only		SBC + TF	
0.70	15.4	0.16	4	0.05	14	-0.02	N/A	-0.10	N/A
0.75	15.2	0.18	4	0.07	10	0.00	265	-0.09	N/A
0.80	14.9	0.20	3	0.09	8	0.03	28	-0.07	N/A
0.85	14.6	0.24	3	0.11	6	0.05	13	-0.05	N/A
0.90	14.1	0.29	2	0.15	5	0.10	7	-0.02	N/A
0.95	13.3	0.37	2	0.22	3	0.18	4	0.04	19

Table 2. The impacts on r_c and population doubling time (D) of reducing targeting fishing mortality rates and shrimp bycatch mortality rates to 2/3 of the 1998 values. These computations were done using steepness of 0.90, the base case value in NOAA (2003).

Scenario	r_c	D (years)
1998 commercial and recreational F estimates ($F_{T,1998}$) and 1998 shrimp bycatch mortality rates ($F_{SBC,1998}$)	-0.02	N/A
67% of $F_{SBC,1998}$ and 100% of $F_{T,1998}$	0.014	51
100% of $F_{SBC,1998}$ and 67% of $F_{T,1998}$	0.033	21
67% of $F_{SBC,1998}$ and 67% of $F_{T,1998}$	0.071	10

The potential biases introduced in computations of intrinsic rate of increase were evaluated by first reducing the plus group from 50 years to 15 years for the calculation of E_0 but leaving the age of senescence at age 60 years. The effects was to produce slightly higher values for r_m and r_c (Table 3).

Table 3. Estimates of the current intrinsic rate of increase (r_c) as a function of Beverton-Holt steepness, shrimp bycatch mortality (SBC) and targeted fishing mortality (TF) but with the plus group in the computation of E_0 being set at 15 years instead of 60 years and the age of senescence in the computation of r_c being kept at age 60 but the age 15+ value for m_x being that for age 15. M is in units of yr^{-1}.

	M_{egg}	r_m	D	r_c	D	r_c	D	r_c	D
steepness				SBC only		TF only		SBC + TF	
0.70	15.3	0.16	4	0.05	14	-0.01	N/A	-0.10	N/A
0.75	15.1	0.18	4	0.07	10	0.01	129	-0.09	N/A
0.80	14.8	0.21	3	0.11	6	0.03	24	-0.07	N/A
0.85	14.5	0.21	3	0.15	5	0.06	11	-0.05	N/A
0.90	14.0	0.30	2	0.21	3	0.11	6	-0.02	N/A
0.95	13.2	0.39	2	0.22	3	0.19	4	0.04	17

Discussion

Demographic theory suggests that r_m reflects the maximum rate of harvest that a population can sustain without decline. The estimates of the maximum intrinsic rate of increase (r_m) for *L campechanus* obtained under values of steepness ranging from 0.70 to 0.95 range from 0.16 to 0.37. These values for r_m indicate that *L. campechanus* could have low to moderate resilience to exploitation (Myers et al. 1999; McAllister et al. 2001) and that the maximum possible harvest rate, above which extinction could be caused, hr_{max}, could range from no higher than 0.37 to 0.16, or lower. Lower values for hr_{max} would result for steepness values less than 0.70

The values implied for the natural mortality rate of eggs are very high. The range from about 13.3 yr^{-1} to 15.4 yr^{-1} for steepness values of 0.95 and 0.70, respectively. In contrast, the assumed rate of natural mortality for age 0 fish when they become susceptible to shrimp trawl bycatch is 0.5 yr^{-1}. (Schirripa and Legault 1999) indicate that age 0 fish first start to show up in shrimp trawl bycatch in about June at lengths of about 5 cm and can be seen at this size in the shrimp trawl bycatch until about October. If spawning starts in May and extends through September as indicated in (Schirripa and Legault 1999), then such fish would be about one month old. If that is the case, then the one-month M_{egg} mortality rate should be multiplied by about 12 to get the annual rate, which become in the order of about $M = 150\ yr^{-1}$. The value of M assumed for month 1 to month 12 should be multiplied by 11/12 giving approximately the same annual rate, though slightly less $M=0.46\ yr^{-1}$). This apparent enormous drop in the rate of natural mortality from the first month (egg to about 5cm length) of life to the period between month 1 and month 12 is striking. How could it be plausible for such an enormously high rate of natural mortality in the first month to fall by a factor of about 300 for months 1 to 12? How certain can the assessments scientists be that the rate of natural mortality from month 1 to month 12 is about $0.5\ yr^{-1}$ and for that matter that M_1 is $0.3\ yr^{-1}$? If the value for M_0 and or M_1 is indeed higher than assumed, then this could lead to considerably different stock assessment results, since the impacts of shrimp trawl bycatch on age 0 and age 1 fish may be considerably different.

The analysis of the relative impacts of targeted fishing and shrimp trawl bycatch on r_c indicated results in contrast to those obtained in (Schirripa and Legault 1999). While the relative impacts appeared to be similar if steepness was very high (0.95), it appeared that for lower steepness values, values for r_c were much lower from the target fishing mortality rates than the shrimp bycatch mortality rates estimated for the year 1998. The doubling time was shorted far more by reducing the targeted fishing mortality rate by a factor of 2/3 than by reducing the shrimp bycatch mortality by a factor of 2/3. Doubling time was also substantially shortened when both mortality factors were reduced by a factor of 2/3. In contrast, in Schirripa and Legault (1999), it was found that targeted fishing had very little impact on the stock rebuilding rates and that recovery rates were far more responsive to potential reductions in shrimp bycatch mortality rates. Moreover, when both sources of mortality were incorporated in the demographic analysis, r_c was positive only for the highest value of steepness, 0.95. The demongraphic analysis results appear to be more pessimistic than the recovery scenarios predicted in (Schirripa and Legault 1999) under similar fishing mortality rates. The reasons for this difference in stock resilience estimates between the demographic analysis and Schirripa and Legault (1999) require further investigation.

The 1999 stock assessment assumed a plus group of 15 years. This could potentially impact stock assessment results because the assumed rate of natural mortality for age 2+ fish is very low, at about $0.1\ yr^{-1}$ and fecundity continues to increase considerably with age even for ages older than 15 years. Although the impacts on r_c were very minor when the plus group age was lowered from 60 to 15 years, it is conceivable that there could be some differences in population dynamics model behaviour if the plus group were to be increased substantially. For example, a 25 year old fish still has about one half the expected unfished reproductive contribution as a 15-year old fish, which has about the maximum unfished reproductive contribution (Figure 7, Schirripa and Legault 1999). Moreover, fish of over 50 years of age have been found in the commercial catch.

In summary, the demographic analysis carried out in this paper raises some questions over a variety of issues in the 1999 stock assessment. First, the estimates of the maximum intrinsic rate for *C. campechanus* are low to moderate compared to other fish species ranging from possibly less than 0.16 to no more than 0.37. This suggests that the stock may be prone to overfishing and can be expected to rebuild at a slow rate unless fishing and bycatch mortality rates are reduced substantially. It is also plausible that with low values for r_m, the stock may be prone to sequential depletion in which many smaller locally concentrated subpopulations are sequentially overfished as the fishery proceeds from one local subpopulation to the next

(Boyer et al. 2001). Second, in contrast to Schirripa and Legault (1999), the demographic analysis suggests that the recovery rate could be substantially higher if the targeted fishing mortality rate was reduced than if the shrimp bycatch mortality was reduced. For example, with steepness at 0.90, a reduction in $F_{T,98}$ by 67% could increase r_c from –0.02 to 0.033 with a doubling time of 21 years. A reduction in FSBC by 67% would increase r_c to only 0.014 with a doubling time of 51 years. A reduction by 67% in both sources of mortality would boost r_c to 0.071 with a doubling time of 10 years. Third, the rate of natural mortality of the very youngest stage (up to about 1 month) is far higher than the value for natural mortality rate assumed for the next stage (about one month to one year). This stark difference in the rate of natural mortality is questionable and if the rate of natural mortality at age 0 is truly uncertain, then this uncertainty should be taken into account in the stock assessment modelling and provision of fisheries management advice. Fourth, the plus group in the 1999 stock assessment was only 15 years, and yet, the rate of natural mortality for such older fish is very low and expected reproductive contribution for much older fish is still relatively high. This suggests the sensitivity of stock assessment results to the assumed plus group age should be evaluated. This is despite the fact that results from the demographic model were relatively insensitive to variations in the plus group and age of senescence.

Acknowledgements

This work has been supported by the Pew Institute for Ocean Science, University of Miami. The author is grateful for Pam Baker, Sallie Davis, Jill Jensen, Marianne Cufone and Elizabeth Babcock for helpful discussions and information provided to support the analyses in this work.

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