

Simulations of the Effects of Fishing on the Atlantic Croaker, *Micropogon undulatus*

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ABSTRACT

Parameters of the von Bertalanffy and Beverton-Holt equations were estimated for the Atlantic croaker, *Micropogon undulatus*: $L_{\infty} = 590$ mm, $W_{\infty} = 2491$ g, $K = 0.3113$, $t_0 = -0.0162$ years, $Z = 3.0$, $t_L = 2$ years, $t_p = 0$ years, and $t_c = 0.50-0.85$ years. Magnitudes of the mortality parameters M and F are unknown except that: (1) their total is bounded by $Z = 3.0$, (2) magnitudes of Z apparently have been more or less constant for the last 50 years, and (3) the magnitudes of M , if not currently about 1.5-2.5 or more, must have been that large near the inception of the shrimp fisheries when effort was low. Cohort biomass is a maximum at about 0.75-1.55 years of age for $M = 1.5-2.5$. Yield curves and yield isopleths are presented for a series of t_c and M values.

Simulations of the effects of fishing on croaker inhabiting the Carolinian Province suggest: (1) the magnitudes of maximum sustainable yields (MSY) critically depend on M , (2) for the most likely ranges of M and t_c , Y/R is an asymptotic function of F , F_{MSY} is at least 1.5, and u_{MSY} is at least 47.5%, (3) curves of eumetric fishing and MSY at given t_c are asymptotic in the most likely ranges of M and t_c , either management strategy requires a t_c range of about 0.5-1.0 years, and required F is extremely sensitive to change in t_c , (4) in terms of MSY, overfishing currently occurs only if M is less than about 1.0-1.5 ($v = 32-48\%$), (5) in terms of eumetric fishing, overfishing now occurs unless M is at least 1.5-2.0 ($v = 48-63\%$)—or more depending upon t_c .

Croaker have great biological capacity to resist growth overfishing if given effective mesh-size regulation. Present simulations for croaker seemingly can be extrapolated as a first approximation to the other members of shrimp communities on the continental shelf—including the shrimp—because members of these communities apparently have a common pattern of population dynamics. Present simulations may underestimate F_{MSY} for many species, because $K = 0.3113$ may be an underestimate and $t_L = 2.0$ years may be an overestimate.

INTRODUCTION

The Atlantic croaker, *Micropogon undulatus*, ranges in the western Atlantic from the Gulf of Maine to Argentina (Chao, 1976). This species is one of the most abundant inshore demersal fishes of the northern Gulf of Mexico (Gulf) and of the Atlantic Ocean off the southeastern United States (Gunter, 1938, 1945; Anderson, 1968; Moore, Brusher, and Trent, 1970; Franks et al., 1972; Chittenden and McEachran, 1976).

Croaker, by themselves, have never supported important commercial fisheries in the warm-temperate Carolinian Province, although they have been a major species in industrial-type fisheries (Gunter, 1950; Haskell, 1961; Bearden, 1964; Roithmayr, 1965), and though they have supported important fisheries in cold-temperate waters north of Cape Hatteras, N.C. (Joseph, 1972). Many workers have emphasized the latent fishery potential of the demersal species

inhabiting soft substrates on the continental shelf of the northern Gulf (Haskell, 1961; Roithmayr, 1965; Bullis and Carpenter, 1968). This emphasis has more or less implied that these fishes could support increased fishing. However, yield models have not been applied to assess the effects of harvesting these resources despite the fact that a large fishery directed at shrimp now catches and discards substantial quantities of fish.

This paper estimates parameters of the Beverton-Holt yield equation, uses this model to assess the effects of harvesting croaker in the Carolinian Province, and extrapolates the implications to other members of shrimp communities inhabiting soft substrates on the continental shelf of the northern Gulf. As used herein, fish refers to a demersal species of such shrimp communities. Findings presented herein may not apply to croaker inhabiting waters north of Cape Hatteras, because their population dynamics differ (White and Chittenden, *in press*).

ESTIMATION OF PARAMETERS

The Beverton-Holt equation assesses changes in cohort biomass by balancing off the growth in weight of its individuals against loss in weight due to their mortality. Simulations presented herein are based on the "long-form" of this equation:

$$Y/R = FW_{\infty} e^{-M(t_c - t_r)} \sum_{n=0}^{\infty} \left[\frac{U_n}{F + M + nK} \right] [e^{-nK(t_c - t_0)}] \quad (1)$$

$$[1 - e^{-(F+M+nK)(t_L - t_c)}]$$

Symbols employed for the equation parameters are those of Gulland (1969). Parameter values used in the simulations are summarized in Table 1. The procedures and rationale applied to estimate the parameters follow.

"Growth-Related" Parameters (L_{∞} , K , t_0 , W_{∞})

The von Bertalanffy equation is used to describe growth in weight, although estimation of parameters usually depends on this equation in terms of length:

$$l_t = L_{\infty} [1 - e^{-K(t-t_0)}] \quad (2)$$

Asymptotic length (L_{∞}) and the growth coefficient (K) may be estimated from a relationship such as the equation for the Walford line:

$$l_{t+1} = L_{\infty}(1 - e^{-K}) + e^{-K} l_t \quad (3)$$

in which the x and y variables represent lengths at specified ages. Given estimates of L_{∞} and K , the theoretical age (t_0) at which length would equal zero if growth had always followed the von Bertalanffy pattern can be estimated by solving the von Bertalanffy equation for t_0 :

$$t_0 = t + \frac{1}{K} (\log_e L_{\infty} - 1t/L_{\infty}) \quad (4)$$

Table 1. Summary of the estimated values for the parameters of the Beverton-Holt equation (The rationale behind each estimate is described in the text)

I.	<p>"Growth-Related" Parameters:</p> <p>$W_{\infty} = 2491$ grams</p> <p>$K = 0.3113$</p> <p>$t_0 = -0.0162$ years</p>
II.	<p>Mortality Coefficients</p> <p>$Z = 3.0$</p> <p>$M = \text{varied}$; see text</p> <p>$F = \text{varied}$; see text</p>
III.	<p>Time Parameters</p> <p>$t_L = 2.0$ years</p> <p>$t_r = 0$ years</p> <p>$t_c = 0.50 - 0.85$ years but varied for modeling; see text</p>

Asymptotic weight W_{∞} can be estimated from L_{∞} using a length-weight relationship:

$$w = a l^b \quad (5)$$

Calculation with the Beverton-Holt equation is simplified by assuming isometric growth, so that W_{∞} may be estimated from the length-weight relationship:

$$w = a' l^3 \quad (6)$$

I note that: (1) the estimates that follow for growth parameters are based on only two data points for a Walford line, and (2) it is difficult to apply Walford-type procedures to croaker inhabiting the Carolinean Province. Walford-type procedures assume that the organism lives a sufficiently long life that at least three data points can be generated to permit "reasonably precise" estimation of the slope and y-intercept. However, the typical maximum life span of croaker in the Carolinean Province is only 1 or 2 years (White and Chittenden, *in press*); so that apparently few data points, at best, will ever be available based upon annual growth. A validated scale method of age determination only recently has been developed for croaker (White and Chittenden, *in press*), and average lengths are not yet known for fish older than age II.

To estimate the growth parameters, I chose values of 160 and 275 mm total length (TL) as the average lengths of croaker at ages I and II, respectively. These

choices were made because White and Chittenden (*in press*) reported that croaker were 155-165 mm TL at age I and 270-280 mm TL at age II, based upon length frequency and, especially, scale methods of age determination. To get coordinates for a second data point, I chose a value of 3 mm TL to represent the average length of croaker at age 0 (time of hatching); because the eggs and early post-larvae are about 1-3 mm (Hildebrand and Cable, 1930). Growth of fishes can be divided into two stanzas during life, and the von Bertalanffy equation describes growth during the second stanza (Ricker, 1975; Iles, 1975). By using length at age 0 to develop a second data point, in effect, I assume that the von Bertalanffy equation approximately describes growth throughout life. If this assumption is wrong, the slope of the Walford line (b) may be an overestimate, the related parameter K may be an underestimate, and L_{∞} may be an overestimate.

The slope (b) and y -intercept (a) of the Walford line were estimated as follows:

$$b = \Delta y / \Delta x = \frac{275 - 160}{160 - 3} = 0.7325 \quad (7)$$

$$\frac{160 - a}{3 - 0} = 0.7325 ; a = 157.8025 \quad (8)$$

The fitted equation for the Walford line is:

$$l_{t+1} = 157.80 + 0.7325 l_t \quad (9)$$

From the relationship described by eq. (3) we have:

$$K = -\log_e b = 0.3113 \quad L_{\infty} = a / (1 - b) = 590 \text{ mm} \quad (10) (11)$$

The parameter t_0 was estimated from eq. (4) as $t_0 = -0.0162$ years and $t_0 = -0.0159$ years by substituting, respectively, $t = 1$ year and $t = 2$ years with appropriate l_t for these ages. I chose $t_0 = -0.0162$ years for simulations. The fitted von Bertalanffy equation for growth in length is:

$$l_t = 590 [1 - e^{-0.3113(t+0.0162)}] \quad (12)$$

Asymptotic weight (W_{∞}) remains to be estimated. Several similar length-weight relationships have been published for croaker (Dawson, 1965; Avault et al., 1969; Parker, 1971; White and Chittenden, *in press*). I chose White and Chittenden's regression equation for the modeling herein:

$$\log_{10} Y = -5.26 + 3.15 \log_{10} X \quad (13)$$

where Y is total weight (grams) and X is total length (millimeters). Assuming isometric growth and substituting White and Chittenden's arithmetic means for $\log_{10} Y$ and $\log_{10} X$ into eq. (13), the isometric length-weight relationship is:

$$\log_{10} Y = -4.9162 + 3 \log_{10} X \quad (14)$$

From this, I estimated $W_{\infty} = 2491$ g.

Mortality Rates (Z , M , F , $1-S$, u , v)

Few data exist on mortality rates of croaker. Estimates of the maximum age are about age II-III (Gunter, 1945; Suttkus, 1955; Bearden, 1964; Nelson, 1969; Hansen, 1969; Hoese, 1973), although Arnoldi, Herke, and Clairain (1973) suggested that industrial landings depend on an annual crop of croaker. White and Chittenden (*in press*) observed that the total annual mortality rate ($1-S$) was 96%. They concluded that the typical maximum life span of croaker in the Carolinean Province was only about 1 or 2 years and estimated that the theoretical total annual mortality rate was 90-100%. Therefore, observed and theoretical estimates agree closely.

The annual total instantaneous mortality rate (Z) is related to the annual total mortality rate (Ricker, 1975):

$$1-S = 1-e^{-Z} \quad (15)$$

For simulations, I assumed that $(1-S) = 95\%$, from which $Z = 3.0$.

Instantaneous mortality rates due to fishing (F) and natural causes (M) are not known. Values of F and M were varied over a broad range to derive yield-per-recruit estimates summarized in the figures presented herein. To use the yield isopleth figures, coordinates on the x and y axes (F and t_C , respectively) must be approximated to indicate where the fishery now lies. Estimates of M and F can be made from the relationship (Ricker, 1975):

$$Z = M + F \quad (16)$$

Knowing that $Z = 3.0$, F can be calculated by postulating a value for M and vice versa. I argue in the "General Discussion" that M is or was most probably about 1.5-2.5. Many of the comments made herein are based on that estimate.

It is convenient, and may be more understandable, to express mortality in terms of annual expectations of death (Ricker, 1975) as well as in instantaneous rates. Croaker approximate best Ricker's type 2B fishery for which the following holds:

$$\frac{Z}{1-S} = \frac{F}{u} \quad (17)$$

where u is the annual expectation of death due to fishing. Once F is postulated, u can be estimated because Z and $(1-S)$ are known. The annual expectation of death due to natural causes (v) can be estimated from:

$$(1-S) = u + v \quad (18)$$

Time Parameters (t_r , t_C , t_L)

The time parameters, t_r , t_C , and t_L demarcate the ages of phases of life at the beginning, during, and at the effective end of the post-recruit portion of life (Beverton and Holt, 1957).

The parameter t_L is a more or less arbitrarily chosen estimate of the age when the fishable life span of a year class ends. In effect, members of the cohort older than age t_L make a negligible contribution to the harvest. White and Chittenden (*in press*) concluded that the typical maximum life span of croaker inhabiting the Carolinian Province was about 1 or 2 years and that the typical maximum sizes reported from that area were about 300 mm or less, although some fish of about 330-380 mm have been reported by Pearson (1929), Gunter (1945), Suttkus (1955), Franks et al. (1972), Christmas and Waller (1973), and White and Chittenden (*in press*). Because croaker reach about 270-280 mm TL at age II, realistic estimates of t_L would apparently be 2 or at most 3 years in the Carolinian Province. I chose $t_L = 2$ years for the modeling presented herein.

The parameter t_r represents the mean age at entry to the *area* of the fishery. New recruits may encounter fishing gear, but they are theoretically not captured if $t_r < t_c$. The precise choice of t_r is not important if $t_r < t_c$ (Gulland, 1969). I chose $t_r = 0$ for modeling purposes, and this is probably reasonable. Croaker spawn in the open ocean, not in estuaries (Pearson, 1929; Hildebrand and Cable, 1930). The larvae probably recruit rapidly to the lower portions of the water column affected by trawls, because the young are transported by saline bottom currents and rapidly appear in estuaries (Pearson, 1929; Hildebrand and Cable, 1930; Wallace, 1940; Haven, 1957).

The parameter t_c , termed the mean selection age or mean age at first capture (Gulland, 1969), represents the mean age at entry to the exploited phase of life. The magnitude of t_c depends upon mesh size of the gear and its selection properties. I varied t_c to derive the yield-per-recruit estimates presented herein. To utilize the yield isopleths, t_c must be approximated to indicate where the fishery now lies. The shrimp fishery is probably the dominant fishery now affecting croaker in the Gulf. Texas and Louisiana permit minimum legal stretched-mesh sizes of about 1.5-1.75 inches for shrimping in the Gulf. I estimated, by two procedures described as follows, that t_c is about 0.50-0.85 years for trawls having these mesh sizes.

A. Escapement through the net largely depends on the maximum girth of the fish and the internal perimeter of the mesh (Beverton and Holt, 1957). The maximum girth of croaker is approximately girth at the origin of the dorsal fin. This can be predicted from plots of the regression of girth (Y) on total length (X) calculated for fish 90-360 mm TL (White and Chittenden, *in press*):

$$Y = -11.84 + 0.71 X \quad (19)$$

Table 2A presents estimates of the ages t_c based upon relationships between mesh sizes, mesh perimeter = maximum girth, and total lengths. Total length was converted to age t_c by solving the von Bertalanffy equation (eq. 2) for t :

$$t = t_0 + \frac{1}{K} \left(\log_e \frac{L_\infty}{L_\infty - L_t} \right) \quad (20)$$

Table 2. Values of t_c derived from two estimation procedures

A. Relationships between mesh size, internal perimeter of the mesh, and the length and age of the fish retained.

Stretched Mesh Size	Girth \approx Internal Perimeter (mm)	$l_c \approx$ Total Length of Fish Retained (mm)	$t_c \approx$ Age of Fish Retained (years)
25.40 mm; 1 inch	50.8	88.23	.50
31.75 mm; 1.25 inch	63.5	106.11	.62
38.10 mm; 1.5 inch	76.2	124.00	.74
44.50 mm; 1.75 inch	88.9	141.89	.87
50.80 mm; 2 inch	101.6	159.77	1.00

B. Estimates of l_c (top value in mm) and t_c (bottom value in years) from mesh sizes listed and l_c /Girth ratios.

Stretched Mesh Size	l_c / Girth			
	1.49	1.58	1.69	1.85
25.40 mm; 1 inch	60.6 mm 0.33 yr	64.2 mm 0.35 yr	68.7 mm 0.38 yr	75.2 mm 0.42 yr
31.75 mm; 1.25 inch	75.7 mm 0.43 yr	80.3 mm 0.45 yr	85.9 mm 0.49 yr	94.0 mm 0.54 yr
38.10 mm; 1.50 inch	90.8 mm 0.52 yr	96.3 mm 0.56 yr	103.0 mm 0.60 yr	112.8 mm 0.67 yr
44.45 mm; 1.75 inch	106.0 mm 0.62 yr	112.4 mm 0.66 yr	120.2 mm 0.72 yr	131.6 mm 0.79 yr
50.80 mm; 2.00 inch	121.1 mm 0.72 yr	128.4 mm 0.77 yr	137.4 mm 0.84 yr	150.4 mm 0.93 yr

This treatment assumes that a mesh of given perimeter retains all fish of greater girth. A struggling fish might compress its girth; so that, theoretically, a fish could escape through mesh smaller than the girth of the fish. Counterbalancing this, however, is the probability that the net would be effectively filled by a mass of small fish, thereby reducing opportunities to reach and contact mesh openings, which might also contain gilled specimens. Nearly all the demersal fishes in the northern Gulf are less than 200 mm in length (Chittenden and McEachran, 1976), so that effective clogging of the net probably occurs, and the basic assumption may be reasonable.

B. The mean selection length (l_c) can be estimated (Beverton and Holt, 1957, Sect. 14. 2.3; Gulland, 1969) from the relationship:

$$l_c = m \cdot b \quad (21)$$

where m is the stretch-mesh size and b is termed the selection factor. The selection factor can be approximated (Beverton and Holt, 1957) from the relationships:

$$l_c = m \cdot \left(\frac{\text{Girth}}{m} \right) \left(\frac{l_c}{\text{Girth}} \right) \quad (22)$$

The ratio (Girth/m) is reasonably constant within the length range in which net selection occurs regardless of the shape of the fish (Beverton and Holt, 1957, p. 231). These authors estimated this ratio was 1.69 in plaice and 1.56 in haddock. I chose a value of 1.6 to approximate this ratio for croaker.

The ratio (l_c /Girth) can be approximated from White and Chittenden's (*in press*) length-girth relationship. This ratio is very constant over a broad length range of croaker as follows: 1.49 at 300 mm TL; 1.58 at 150 mm TL; 1.69 at 100 mm TL; and 1.85 at 70 mm TL. I chose each of these ratios to approximate l_c using eq. (21 and 22), and converted l_c to t_c by using eq. (20). Estimates for t_c derived in this fashion (Table 2B) are lower, although they agree closely with estimates derived by the first procedure.

GENERAL EFFECTS OF FISHING ON CROAKER

The magnitudes of the maximum sustainable yields (MSY) that can be obtained from croaker depend critically on the magnitude of M . This is illustrated by yield-per-recruit (Y/R) curves as a function of F for my estimates of the current ages at first capture ($t_c = 0.50, 0.75$ in Fig. 1). Maximum values of Y/R range from about 3-40 g and are inversely related to the magnitude of M . In general, values for MSY are comparatively negligible if M is as high as 2.5. Even within the range $M = 1.5-2.5$, Y/R at $M = 1.5$ is double or triple that possible at $M = 2.5$. The croaker life span is so short and the higher graphed values of M are so large that comparatively many croaker die during the period $t_r - t_c$, which occurs before they theoretically can be captured. Similarly, after age t_c , the life span is so short and these M values are so large in relation to K that a cohort of fish has little opportunity to increase its biomass.

The shape of the yield curves is very important. Values of Y/R increase to an asymptote in the parameter ranges $M = 1.5-2.5$ and $t_c = 0.50-0.75$ (Fig. 1). Furthermore, MSY is achieved when F is no lower than 1.5; so that MSY is achieved only at $u > 47.5\%$. There is little if any decrease in Y/R beyond F_{MSY} even if F ranges to 5.0, a value which greatly exceeds the estimated Z . For older t_c , F_{MSY} is higher and may even exceed $F = 5.0$. If F_{MSY} is exceeded, the catch might decrease, but only for $t_c = 0.25$ yr or for $M < 1.50$ at young t_c . Because of the asymptotic nature of the yield curves, croaker evidently have great biological capacity to withstand growth overfishing if given effective mesh-size regulation.

The concept of optimum sustainable yield permits MSY as an objective (Roedel, 1975), but this may be economically irrational for croaker. The yield curves as a function of F (Fig. 1) express the economics of the fishery assuming that Y/R is proportional to the value of the catch and that F is proportional to the cost of fishing (Gulland, 1974). Under these circumstances, MSY also represents the maximum gross economic yield. Fishing effort greater than that at F_{MSY} would not affect the value of the catch but could greatly increase the cost of fishing. Maximum net economic yield, and profit, occurs at some F lower than F_{MSY} . Eumetric management (Beverton and Holt, 1957) implies that a given Y/R or value of the catch can be achieved by different combinations of mesh size (which determines t_c) and fishing effort (which is proportional to F).

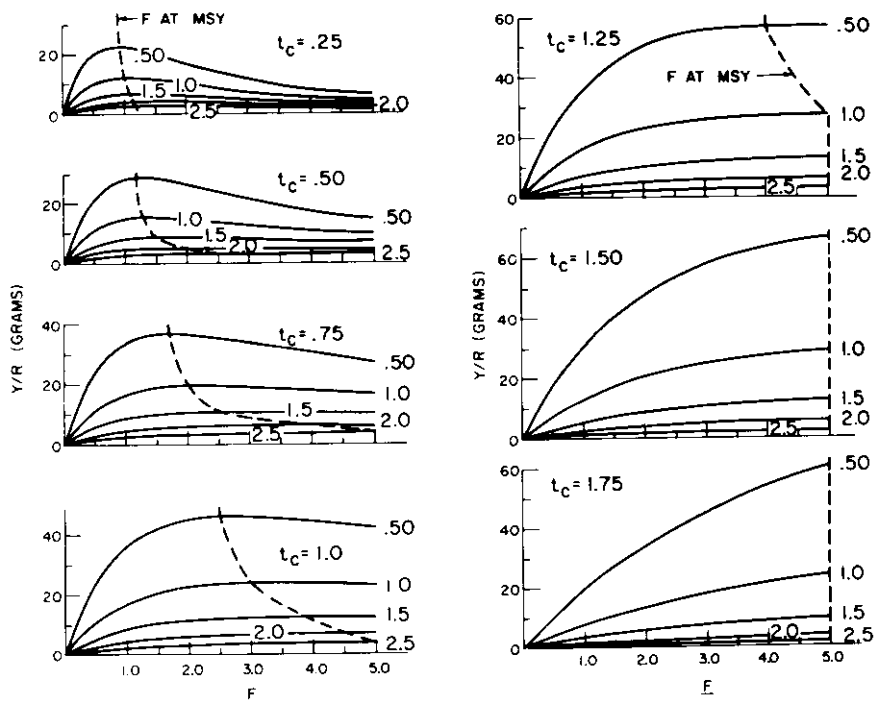


Fig. 1. Yield/recruit (Y/R) as a function of F for $t_L = 2.0$ years at listed values of M and t_c . Individual curves are listed for values of M .

The combined effects of mesh size and fishing effort can be expressed as yield isopleths which describe eumetric fishing combinations and MSY at any chosen t_c (Figs. 2-6). The yield contours drawn are very sensitive to slight graphing errors. However, in general, a given yield may be attained with much less effort and cost of fishing under eumetric conditions than by fishing for MSY .

The shape of the eumetric fishing curve (BB') and the curve of MSY (AA') is very important. The slope of the curve greatly decreases with increasing t_c . As a result, the curves approach an asymptote in the parameter ranges $t_c = 0.50-1.0$ and $M = 1.5-2.5$. The asymptote is approached earlier in life (e.g. -at lower values of t_c) as M increases. Management for eumetric conditions or MSY evidently must be delicately balanced and would be difficult to achieve exactly, because slight absolute changes in t_c require large change in F to remain on the curves. Small absolute changes in t_c are large relative changes, because the croaker life span is so short and M is apparently so high. Management under a eumetric or MSY strategy would require a t_c range of about 0.5-1.0 years or less if $M \cong 1.5-2.5$, although croaker of the Carolinean Province do not spawn until the end of their first year (White and Chittenden, *in press*; Hansen, 1969).

CURRENT EFFECTS OF FISHING ON CROAKER

The current effects of fishing on croaker can be assessed from the yield isopleths. My assessment assumes that $t_c = 0.50-0.85$ years and postulates values of M and F . However, the shapes of the yield curves and isopleths presented herein are probably valid, because they depend only on values of K , t_0 , W_∞ and t_L . Choice of the appropriate curve or isopleth and the location of appropriate points on the graphs depend on values of t_c , M , and F ; therefore, interpretation of the figures may change as knowledge of these parameters is refined.

If $M = 0.5$ or 1.0 , then $F = 2.50$ or 2.0 , respectively. With these parameter values we must conclude that croaker are currently grossly over-fished in the eumetric sense and in terms of MSY (Figs. 2, 3). An alternative conclusion is that $M > 1.0$, $\nu > 32\%$, and that croaker may not be overfished.

If $M = 1.5$, then $F = 1.5$. We conclude that croaker are currently underfished in terms of MSY but grossly overfished in the eumetric sense (Fig. 4). For $t_c = 0.75$, eumetric fishing requires half the current fishing effort. However, the degree of overfishing depends critically on the value of t_c . If croaker are not currently overfished in the eumetric sense, we must conclude that $M > 1.50$ and $\nu > 48\%$.

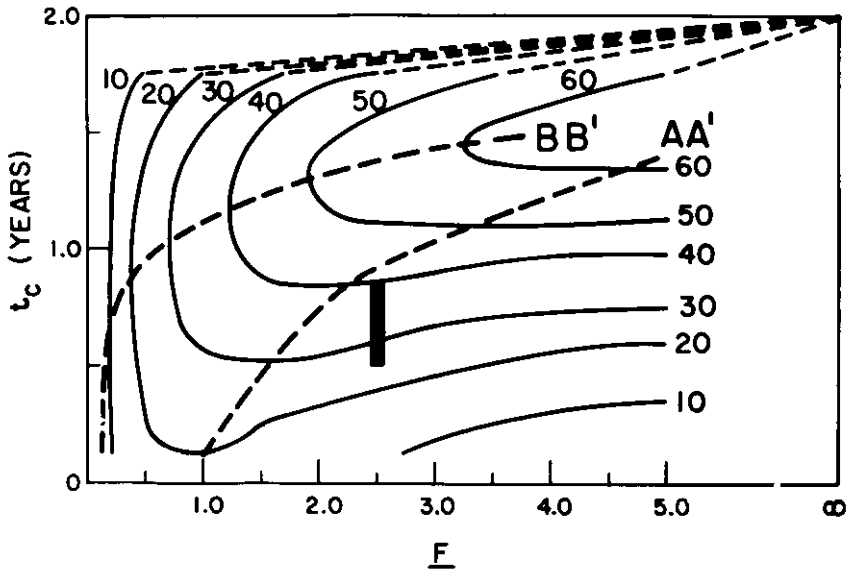


Fig. 2. Yield isopleths summarizing Y/R (grams) for $t_L = 2.0$ years and $M = 0.50$. Isopleths represent listed magnitudes of Y/R . Curve BB' represents the curve of eumetric fishing and AA' represents the curve of maximum sustainable yield at each value of t_c (Beverton, 1953). The darkened rectangle represents the current position of the fishery if $M = 0.50$.

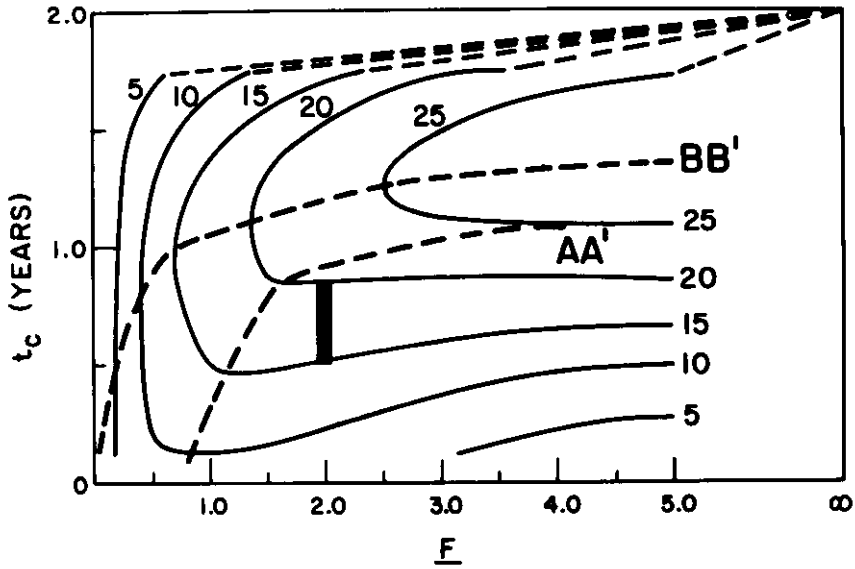


Fig. 3. Yield isopleths summarizing Y/R (grams) for $t_L = 2.0$ years and $M = 1.0$. The darkened rectangle represents the current position of the fishery if $M = 1.0$.

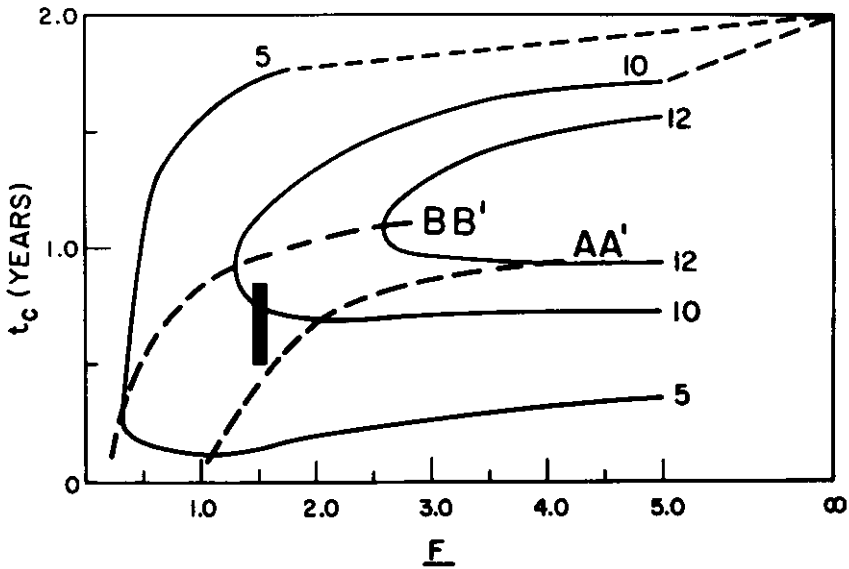


Fig. 4. Yield isopleths summarizing Y/R (grams) for $t_L = 2.0$ years and $M = 1.50$. The darkened rectangle represents the current position of the fishery if $M = 1.50$.

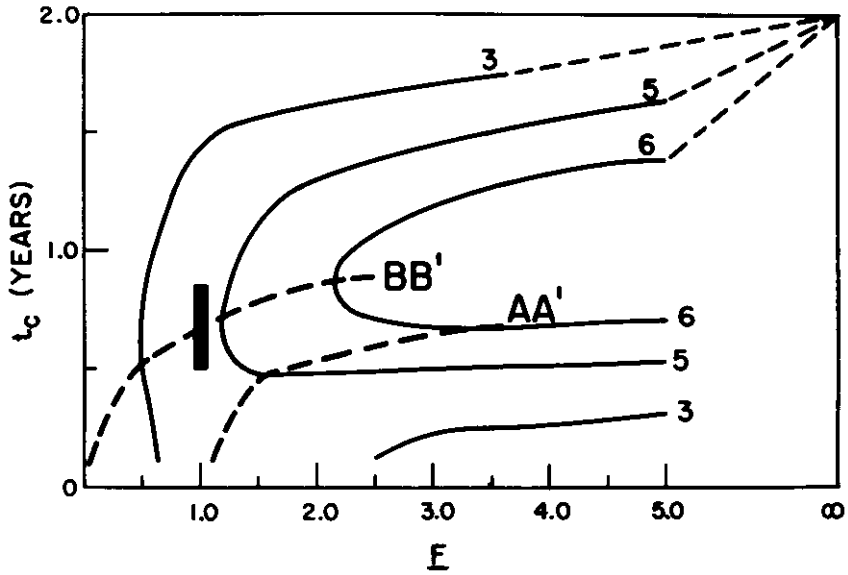


Fig. 5. Yield isopleths summarizing Y/R (grams) for $t_L = 2.0$ years and $M = 2.0$. The darkened rectangle represents the current position of the fishery if $M = 2.0$.

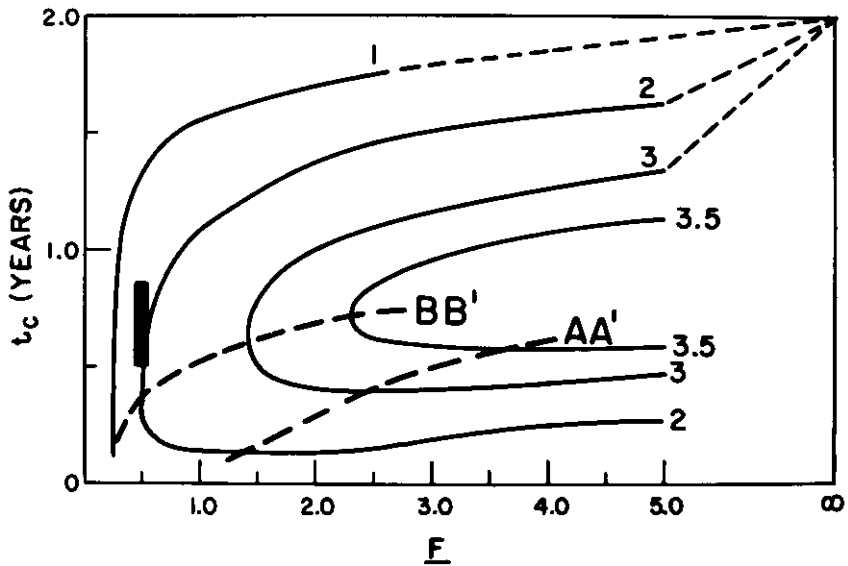


Fig. 6. Yield isopleths summarizing Y/R (grams) for $t_L = 2.0$ years and $M = 2.50$. The darkened rectangle represents the current position of the fishery if $M = 2.50$.

If $M = 2.0$, then $F = 1.0$, $v = 63\%$ and $u = 32\%$. We conclude that croaker are currently underfished in terms of MSY and that fishing is reasonably near eumetric conditions (Fig. 5). However, the latter conclusion is extremely sensitive to slight changes in t_c , because the slope of the curve BB' changes so rapidly within my estimated range for the current t_c . If $t_c \cong 0.85$, effort should be approximately doubled to reach eumetric conditions; but effort should be reduced by half if $t_c \cong 0.50$.

If $M = 2.5$, then $F = 0.50$, $v = 79\%$ and $u = 16\%$. We conclude that croaker are grossly underfished in both the eumetric sense and in terms of MSY (Fig. 6). However, a 16% annual expectation of death due to fishing is often considered a low fishing mortality and may be unrealistically low because the current fishery is so large. Texas alone annually licenses more than 3000 vessels for shrimping, and about 2000 of these are Gulf vessels (O. Farley and T. Leary, *pers. communications*).

Exact assessment of the current impact of fishing is not possible because M is unknown. However, we must conclude that croaker are overfished in terms of MSY only if v is less than some value in the range 32-48%. In terms of eumetric fishing, we must conclude that croaker are grossly overfished unless v is greater than some value in the range 48-63%. Depending upon the value of t_c , gross overfishing may occur even if $v = 63\%$.

GENERAL DISCUSSION

The demersal fishes inhabiting soft substrates on the continental shelf of the Gulf form more or less distinct faunal assemblages which have been described as white, brown, and pink shrimp communities (Hildebrand, 1954, 1955; Chittenden and McEachran, 1976). The abundant species of the white and brown shrimp communities, at least, or the communities, apparently have evolved towards a more or less common pattern of population dynamics which stresses small size (fish smaller than 200 mm in length), rapid completion of life (90-100% total annual mortality rate), high turnover of biomass, and great biological capacity to withstand growth overfishing. The literature supports these general conclusions; because many other workers have made similar observations or conclusions about one or more of these fishes, especially fishes of the white shrimp community (Gunter, 1938, 1945; Hildebrand, 1954; Haskell, 1961; Roithmayr, 1965; Bullis and Carpenter, 1968; Chittenden and McEachran, 1976). The general features of population dynamics stated might apply to the fishes of the pink shrimp community, as well, because Hildebrand (1955) observed only small fishes in this community off Mexico. However, additional data are needed about the composition and dynamics of that fauna. This general pattern may also apply to the shrimp, because they are small and have typical life spans of about 1.5-2 years (see Cook and Lindner, 1970; Costello and Allen, 1970; Lindner and Cook, 1970).

If a common pattern of population dynamics exists, then implications of the present simulations for croaker can be extrapolated as a first approximation to the other abundant species. Basic responses to fishing are determined in the

Beverton-Holt model by the mortality rate M and the growth parameter K which together determine the trend with age in cohort biomass. The mortality and growth parameters each appear reasonably consistent among the abundant fishes; although much more work is needed, especially on growth. However, differences important to management may occur between species because of variation in their effective t_C values. The simulations presented herein may be conservative for many species in that the simulations probably underestimate F values required to achieve MSY . The reason for this is that, for many species, the values of t_L and/or K chosen for simulation herein are probably an overestimate and underestimate, respectively. Both forms of error would result in underestimation of F_{MSY} (Beverton and Holt, 1957). Therefore, many species may be less susceptible to overfishing than my simulations suggest.

Values for the time of maximum biomass (t_{MB}) are consistent over a broad range of mortality and growth values, so that it seems probable that these parameters are sufficiently alike that croaker modeling will apply to the whole communities as a first approximation. The potential yield from a cohort is age-dependent. The cohort reaches a maximum biomass at an age when its survivors average some "critical size" (Ricker, 1945) at which rates of growth and mortality balance and when the cohort should be immediately harvested. The age when cohort biomass is a maximum can be estimated (Alverson and Carney, 1975) from the equation:

$$t_{MB} = (1/K) \log_e [(M+3K)/M] \quad (23)$$

For constant M values in the range 1.5-2.5, values of t_{MB} for croaker vary only slightly even if K is half, double, triple or quadruple the K value used herein for simulations (Table 3). The values of t_{MB} vary only from 0.7-1.7 years regardless of the M and K values tabulated.

The mortality parameters M and F are bounded by the magnitude of Z , and this provides insight into the magnitudes of M and F . Current values of Z and typical maximum life spans seemingly have not changed greatly, if at all, in many years. They must now be quite uniform for the abundant fishes, because the fish typically live only about 1 or 2 years. The recent maximum sizes of the abundant fishes on the white and brown shrimp grounds are very similar to maxima reported in the literature (Chittenden and McEachran, 1976). Recent size compositions and species compositions (Chittenden and McEachran, 1976)

Table 3. Values of t_{MB} for listed values of M and K

K	M		
	1.50	2.00	2.50
0.1500	1.75 (yr)	1.35 (yr)	1.10 (yr)
0.3113	1.55	1.23	1.02
0.6000	1.42	1.07	0.90
0.9000	1.14	0.95	0.81
1.2000	1.02	0.88	0.74

also seem consistent with those reported by Gunter (1938, 1945) and Hildebrand (1954) early in the history of the white and brown shrimp fisheries. It is important that 30-50 years ago Pearson (1929) and Gunter (1938, 1945) suggested that some fishes of the white shrimp community, such as *Cynoscion nothus*, *Leiostomus xanthurus*, *Micropogon undulatus*, and *Stellifer lanceolatus*, "disappeared" or perished after 1 or 2 years or had "short life cycles." Therefore, it seems reasonable to conclude that Z and t_L have remained more or less constant since that time; although short life spans and non-random sampling could hide important relative changes in sizes, numbers, or species compositions. If Z has been reasonably constant, M must have been about 1.5-2.5 or more early in the history of the shrimp fisheries when fishing effort was low. If Z has been reasonably constant, we must conclude either: (1) the magnitude of F is now and always has been very small and that M is now and always has been very large, or (2) the magnitude of F may now be large and that M may be very plastic within the bounds of a more or less constant Z . A plastic M and more or less constant Z could mean that regulation of t_c and F would automatically result in a new M , a new set of parameter relationships, need for new regulation, and a difficult management situation.

Little is known about comparative magnitudes of the growth parameters K , W_∞ , and t_0 , and this may be the greatest weakness in extrapolating the current simulations. However, the apparent facts that typical maximum life spans are similar and sizes are small suggests that values of the growth parameters are reasonably similar among fishes of the white and brown shrimp communities. Absolute growth evidently differs between the important fishes (Table 4), so that values of L_∞ and W_∞ probably vary between species. However, assuming constant M and K , between species variation in W_∞ implies only that magnitudes of Y/R differ between species. The shape of the yield curves would not differ (Alverson and Carney, 1975), and this determines the effects of fishing. Crude estimates of lengths at age 1 (Table 4) suggest that the abundant fishes of the white shrimp community are larger at age than the abundant fishes of the brown shrimp community. If this is true, it would suggest that: (1) Y/R values may be higher for the fishes of the white shrimp community assuming M and K are consistent among species, or (2) the magnitudes of K and/or M may exhibit consistent differences between the communities.

The *effective* mean ages at first capture probably vary among the abundant species, and this may cause important differences in their actual responses to fishing. Simulations showed that a slight absolute change in t_c requires large change in F to remain on the curves of eumetric fishing or fishing for *MSY*. Although t_c theoretically depends upon girth and mesh size, in a practical sense the important factor may be the age when a fishery is first imposed. Therefore, an effective t_c may vary greatly among species, because their spawning seasons vary. The effective t_c would depend upon which member of the shrimp community that fishing or management is directed at. Evidently, an "optimal" or *MSY*-based management plan for a multiple-species fishery, or a directed fishery such as the shrimp fishery, could impose excessive effort on some species and too little effort on others.

Table 4. Approximate fork lengths (mm) at age I of abundant fishes of the white and brown shrimp communities (Estimates are from the text or length-frequency graphs of Chittenden and McEachran (1976); asterisks indicate total length)

Species	Most Typical Of	
	White Shrimp Community	Brown Shrimp Community
<i>Arius felis</i>	110-130	--
<i>Halieutichthys aculeatus</i>	--	60-85 (Max = 92)
<i>Serranus atrobranchus</i>	--	60-90
<i>Stenotomus caprinus</i>	--	80-110
<i>Cynoscion arenarius</i>	120-180 (at least)*	--
<i>Cynoscion nothus</i>	150-185*	--
<i>Micropogon undulatus</i>	155-165*	--
<i>Stellifer lanceolatus</i>	80-125*	--
<i>Upeneus parvus</i>	--	80-145 (?)
<i>Polydactylus octonemus</i>	105-145 (at least)	--
<i>Peprius burri</i>	95-120	--
<i>Bellator militaris</i>	--	65-110
<i>Prionotus paralatus</i>	--	80-125
<i>Syacium gunteri</i>	--	80-130

The demersal fishes of the shrimp communities seemingly have a great biological capacity to withstand overfishing. However, two kinds of overfishing can be distinguished (Cushing, 1976): (1) growth overfishing in which the fish are harvested at too small a size and the maximum cohort biomass is not permitted to develop, and (2) recruitment overfishing in which parent stocks are so reduced that progeny stocks also decline. The Beverton-Holt model employed herein assumes that no spawner-recruit relationship exists within the range of stock sizes fished. Therefore, the simulations presented herein indicate only a great capacity to withstand growth overfishing. Spawner-recruit relationships of the fauna of the shrimp communities need study, although abundance of short-lived species is often considered to be largely density-independent.

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