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Douglas S. Vaughan Eldon J. Levi Joseph W. Smith

U.S. Department of Commerce

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Ronald H. Brown Secretary

National Oceanic and Atmospheric Administration

D. James Baker Under Secretary for Oceans and Atmosphere

National Marine Fisheries Service

Rolland A. Schmitten Assistant Administrator for Fisheries



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Population Characteristics of Gulf Menhaden, Brevoortia patronus

DOUGLAS S. VAUGHAN, ELDON J. LEVI, and JOSEPH W. SMITH

National Marine Fisheries Service Beaufort Laboratory 101 Pivers Island Road Beaufort, North Carolina 28516-9722

ABSTRACT

The status of the gulf menhaden, Brevoortia patronus, fishery was assessed with purseseine landing data from 1946 to 1992 and port sampling data from 1964 to 1992. These data were analyzed to determine growth rates, biological reference points for fishing mortality from yield per recruit and maximum spawning potential analyses, spawner-recruit relationships, and maximum sustainable yield (MSY). Virtual population approaches were used to obtain point estimates of stock size, recruits to age 1, spawning stock size, and fishing mortality rates. Exploitation rates ranged between 14% and 45% for age-1 fish, between 30% and 72% for age-2 fish, and between 36% and 71% for age-3 fish. Biological reference points from yield per recruit (F_{0.1}: 0.7–0.9 yr⁻¹) and maximum spawning potential (F₂₀: 1.6– 2.9 yr⁻¹ and F_{30} : 1.0–2.1 yr⁻¹) were obtained for comparison with recent estimates of F (0.4–0.8 yr⁻¹). Parameters from Ricker-type spawner-recruit relations were estimated, although considerable unexplained variability remained. Estimates of long-term MSY from fits of the generalized production model ranged between 664,000 metric tons (t) and 897,000 t. Declines in landings since 1988 have raised concerns about the status of the gulf menhaden stock. However, gulf menhaden are short lived and highly fecund. Thus, variation in recruitment to age 1 largely mediated by environmental conditions influences fishing success over the next two years (as age-1 and age-2 fish). Comparisons of recent estimates of fishing mortality to biological reference points do not suggest overfishing.

Introduction

Gulf menhaden, Brevoortia patronus, is a euryhaline species found in coastal and inland tidal waters from the Yucatan Peninsula in Mexico to Tampa Bay, Florida (Nelson and Ahrenholz, 1986; Christmas et al., 1988). Adult menhaden are filter feeders (feeding primarily on phytoplankton) and, in turn, support predatory fishes. Gulf menhaden form large surface schools which appear in nearshore Gulf waters from about April to November. Although no extensive coastwide migrations are known to occur, there is evidence that older fish move toward the Mississippi River delta (Ahrenholz, 1981). Spawning peaks during December and January in offshore waters (Lewis and Roithmayr, 1981). Eggs hatch at sea and the larvae are carried to estuaries by ocean currents where they develop into juveniles (Christmas et al., 1988). Juveniles migrate offshore during winter and move back to coastal waters the following spring as age-1 adults.

Gulf menhaden are subject to an extensive purseseine fishery in the northern Gulf of Mexico from midApril through mid-October that is regulated by interstate compact (Christmas et al., 1988). Since 1964, the National Marine Fisheries Service has maintained a sampling program for gulf menhaden. During this period the number of active reduction plants where menhaden are processed for meal and oil has varied between 6 and 14, with 6 plants active in 1992 (Table 1). The number of purse-seine vessels has varied between 51 and 92, with 51 vessels active during the 1992 fishing season. Annual landings and nominal fishing effort (vessel-ton-weeks), available since 1946, show an upward trend in landings from 1946 through 1984 when landings peaked at 982,800 t (Fig. 1). Nominal effort peaked the previous year (1983) at 655,800 vessel-tonweeks. Since that time, landings and nominal effort have declined to 421,400 t and 408,000 vessel-ton-weeks in 1992. Between 1984 and 1992, the number of reduction plants declined from 11 to 6 and the number of purse-seine vessels from 81 to 51.

Detailed information on daily vessel landings and fish sampled for length, weight, and age (from scales) is

Number of gulf menhaden, *Brevoortia patronus*, reduction plants by port, total number of purse-seine reduction vessels, and number of fish sampled for age and size for fishing years 1964–92.

| Fishing | | Ports | | | | | | | | No. | No. |
|---------|---|-------|---|---|----|----|---|----|--------|---------|---------|
| year | А | MP | E | D | MC | IC | С | SP | plants | vessels | sampled |
| 1964 | 0 | 3 | 2 | 2 | 1 | 0 | 2 | 1 | 11 | 78 | 12,457 |
| 1965 | 0 | 3 | 2 | 3 | 1 | 1 | 2 | 1 | 13 | 87 | 15,819 |
| 1966 | 1 | 3 | 2 | 2 | 1 | 1 | 2 | 1 | 13 | 92 | 13,016 |
| 1967 | 0 | 3 | 2 | 2 | 1 | 1 | 3 | 1 | 13 | 85 | 14,519 |
| 1968 | 1 | 3 | 2 | 2 | 1 | 1 | 3 | 1 | 14 | 78 | 16,499 |
| 1969 | 1 | 3 | 2 | 1 | 1 | 1 | 3 | 1 | 13 | 75 | 15,281 |
| 1970 | 0 | 3 | 2 | 2 | 1 | 1 | 3 | 1 | 13 | 76 | 10,560 |
| 1971 | 0 | 3 | 2 | 2 | 1 | 1 | 3 | 1 | 13 | 85 | 7,859 |
| 1972 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 75 | 10,030 |
| 1973 | 0 | 2 | 2 | 1 | 1 | 1 | 3 | 0 | 10 | 66 | 8,958 |
| 1974 | 0 | 2 | 2 | 1 | 1 | 1 | 3 | 0 | 10 | 71 | 10,120 |
| 1975 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 78 | 9,529 |
| 1976 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 82 | 13,586 |
| 1977 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 80 | 14,918 |
| 1978 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 80 | 12,985 |
| 1979 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 78 | 11,620 |
| 1980 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 79 | 9,961 |
| 1981 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 80 | 10,408 |
| 1982 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 82 | 10,709 |
| 1983 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 81 | 14,840 |
| 1984 | 0 | 3 | 2 | 1 | 1 | 1 | 3 | 0 | 11 | 81 | 16,001 |
| 1985 | 0 | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 7 | 73 | 13,240 |
| 1986 | 0 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 8 | 72 | 16,530 |
| 1987 | 0 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 8 | 75 | 16,530 |
| 1988 | 0 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 8 | 73 | 12,410 |
| 1989 | 0 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 9 | 77 | 13,970 |
| 1990 | 0 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 9 | 75 | 11,670 |
| 1991 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 7 | 58 | 11,690 |
| 1992 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 6 | 51 | 15,590 |

A = Appalachicola, FL. Reduction plant: Fish Meal Co. (1966, 1968-69).

MP = Moss Point, MS. Reduction plants: Seacoast Products Co. (1964–72, 1975–84), AMPRO Fisheries, Inc. [formerly Standard Products] (1964–90), Zapata Haynie, Inc. (1964–92).

E = Empire, LA. Reduction plants: Empire Menhaden Co. (1964–91), Daybrook Fisheries [formerly Petrou Fisheries, Inc.] (1964–92). D = Dulac, LA. Reduction plants: Dulac Menhaden Fisheries (1964–68, 1970–71), Fish Meal and Oil Co. (1964–65), Zapata Haynie, Inc. (1965–92).

MC = Morgan City, LA. Reduction plants: Seacoast Products Co. (1965-84), Gulf Protein (1989-92).

IC = Intracoastal City, LA. Reduction plants: Seacoast Products Co. (1965-84), Zapata Haynie, Inc. (1985-92).

C = Cameron, LA. Reduction plants: Louisiana Menhaden Co. (1964–90), Seacoast Products Co. (1964–84), Zapata Haynie, Inc. (1967–92).

SP = Sabine Pass, TX. Reduction plant: Texas Menhaden Co. (1964–71).

available from 1964 to the present. This information was used to estimate the number of fish landed at age from 1964 to 1992 (Table 2). The fishery depends primarily on age-1 fish (representing 44% to 92% of the landings) and on age-2 fish (7% to 53%) (Fig. 2). The remaining ages (age-0, age-3, and age-4+) generally contribute insignificantly to the landings (<1% to 13%), although age-3 contributed 10% in 1975. In some years age-2 menhaden account for almost 50% of the

landings, presumably because the cohort represented by the age-2 fish is strong relative to the subsequent cohort (i.e. age-1 fish).

Vaughan (1987) last analyzed coastwide gulf menhaden data for fishing years 1964–85. However, landings have declined sharply since then. The purpose of this paper is to reevaluate the status of the gulf menhaden stock using seven additional fishing years (through fishing year 1992). The analyses that follow parallel to

Estimated landings of gulf menhaden, *Brevoortia patronus*, in numbers at age (0-4+), total numbers landed (ages 0-4+), total landings by weight, and nominal fishing effort (vessel-ton weeks) for the fishing years, 1964–92.

| | | Landings in no. at age (10 ⁹) | | | | | | | |
|-----------------|------|---|------|------|------|-------|-----------|--------------------------------|--|
| Fishing year | 0 | 1 | 2 | 3 | 4+ | Total | (1,000 t) | fishing effort ¹ | |
| 1964 | 0.0 | 3.33 | 1.50 | 0.12 | 0.0 | 4.95 | 409.4 | 272.9 | |
| 1965 | 0.04 | 5.03 | 1.08 | 0.08 | 0.0 | 6.23 | 463.1 | 335.6 | |
| 1966 | 0.03 | 3.31 | 0.87 | 0.03 | 0.0 | 4.24 | 359.1 | 381.3 | |
| 1967 | 0.02 | 4.27 | 0.34 | 0.01 | 0.0 | 4.64 | 317.3 | 404.7 | |
| 1968 | 0.07 | 3.48 | 1.00 | 0.04 | 0.0 | 4.58 | 373.5 | 382.3 | |
| 1969 | 0.02 | 6.08 | 1.29 | 0.03 | 0.0 | 7.41 | 523.7 | 411.0 | |
| 1970 | 0.05 | 3.28 | 2.28 | 0.04 | 0.0 | 5.65 | 548.1 | 400.0 | |
| 1971 | 0.02 | 5.76 | 1.96 | 0.18 | 0.0 | 7.92 | 728.2 | 472.9 | |
| 1972 | 0.02 | 3.05 | 1.73 | 0.09 | 0.0 | 4.89 | 501.7 | 447.5 | |
| 1973 | 0.05 | 3.03 | 1.11 | 0.10 | 0.0 | 4.29 | 486.1 | 426.2 | |
| 1974 | 0.0 | 3.85 | 1.47 | 0.06 | 0.0 | 5.38 | 587.4 | 485.5 | |
| 1975 | 0.11 | 2.44 | 1.50 | 0.46 | 0.0 | 4.51 | 542.6 | 538.0 | |
| 1976 | 0.0 | 4.59 | 1.37 | 0.20 | 0.0 | 6.17 | 561.2 | 575.8 | |
| 1977 | 0.0 | 4.66 | 1.33 | 0.11 | 0.01 | 6.11 | 447.1 | 532.7 | |
| 1978 | 0.0 | 6.79 | 2.74 | 0.05 | 0.01 | 9.59 | 820.0 | 574.3 | |
| 1979 | 0.0 | 4.70 | 2.88 | 0.34 | 0.01 | 7.92 | 777.9 | 533.9 | |
| 1980 | 0.07 | 3.41 | 3.26 | 0.44 | 0.05 | 7.22 | 701.3 | 627.6 | |
| 1981 | 0.0 | 5.75 | 1.42 | 0.33 | 0.03 | 7.54 | 552.6 | 623.0 | |
| 1982 | 0.0 | 5.15 | 3.30 | 0.50 | 0.06 | 9.01 | 853.9 | 653.8 | |
| 1983 | 0.0 | 4.69 | 3.81 | 0.38 | 0.03 | 8.90 | 923.5 | 655.8 | |
| 1984 | 0.0 | 7.75 | 2.88 | 0.44 | 0.05 | 11.12 | 982.8 | 645.9 | |
| 1985 | 0.0 | 8.13 | 2.72 | 0.28 | 0.02 | 11.15 | 881.1 | 560.6 | |
| 1986 | 0.0 | 4.26 | 5.04 | 0.18 | 0.03 | 9.51 | 822.1 | 606.5 | |
| 1987 | 0.0 | 5.94 | 4.53 | 0.40 | 0.01 | 10.87 | 894.2 | 604.2 | |
| 1988 | 0.0 | 5.57 | 2.80 | 0.16 | 0.01 | 8.55 | 623.7 | 594.1 | |
| 1989 | 0.0 | 5.98 | 1.56 | 0.06 | 0.0 | 7.61 | 569.6 | 555.3 | |
| 1990 | 0.0 | 3.93 | 1.89 | 0.14 | 0.01 | 5.97 | 528.3 | 563.1 | |
| 1991^{2} | 0.0 | 2.10 | 2.38 | 0.25 | 0.03 | 4.77 | 544.3 | 472.3 | |
| 1992^{2} | 0.0 | 2.16 | 1.49 | 0.22 | 0.03 | 3.90 | 421.4 | 408.0 | |

¹ Units are 1,000 vessel-ton weeks.

² Preliminary estimates of catch in numbers at age for 1991 and 1992 fishing years.

some extent those presented in Nelson and Ahrenholz (1986) and Vaughan (1987) with modifications as described. Estimates of population numbers and fishing mortality rates by age are obtained from virtual population analysis (VPA). For each fishing year, length at age is estimated by fitting the von Bertalanffy growth curve to obtain parameter estimates; weight at age is obtained by relating weight to length. Biological reference levels of fishing mortality are obtained from yield per recruit and spawning stock biomass per recruit approaches. Spawning stock biomass is compared with subsequent recruitment to age 1, from which Ricker spawner-recruit model parameters are estimated. Effective fishing effort is obtained by adjusting nominal effort for estimated variability in the catchability coefficient, from which parameters for the Pella-Tomlinson generalized production models are estimated (with annual landings data) and used to estimate maximum sustainable yield (MSY). The results from these models are used to evaluate the status of the gulf menhaden stock.

Methods _

Two general methods of virtual population analysis are used in this assessment. The first method, that of Murphy (1965), is described in Vaughan (1987). In applying this method, the calendar year was divided into four periods (or quarters) of approximately equal duration as described in Nelson and Ahrenholz (1986), with the first quarter beginning on 1 January. Catches in numbers at age were summarized quarterly. The annual instantaneous natural mortality rate (M) was estimated from analysis of mark-recapture data (Ahrenholz, 1981).

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This estimate (1.1 per year or 0.275 per quarter) was assumed constant for all ages (>0.5) and years. Because of uncertainties in ageing, especially older fish (Nicholson and Schaaf, 1978), estimates of fish older than age 4 in the landings were assumed to be unreliable. Therefore, fish older than age 4 were pooled with age-4 fish. As in Nelson and Ahrenholz (1986) and Vaughan (1987), estimates of the annual instantaneous fishing mortality rate (F_i) for age-2 fish were derived separately for each year class (cohort) by comparing catches of age-2 and age-3 fish,



Figure 1

Landings and nominal fishing effort by the gulf menhaden, *Brevoortia patronus*, reduction fishery, 1946–92.



Figure 2

Percent of numbers for ages 1–4+ gulf menhaden, *Brevoortia patronus*, estimated from landings by the reduction fishery, 1964–92.

$$F_i = (\ln C_i - \ln C_{i+1}) - M, \tag{1}$$

where *C* is the annual catch in numbers at age (*i* or *i*+1), and *M* is the instantaneous natural mortality rate. This procedure assumes equal selectivity for ages 2 and 3 and that fishing mortality rates are approximately equal for adjacent fishing years. Initial terminal values of *F* for the oldest age group landed in a year class (or cohort) were adjusted by trial and error until the sum of the quarterly *F*'s for age-2 fish was nearly equal to the annual estimates of F_2 obtained from Equation 1 (Table 3). Estimates of population size and fishing mortality rates were made only through the 1989 year class (age 1 in 1990, age 2 in 1991, and age 3 in 1992), so estimates of population size, recruits to age 1, and fishing mortality for age 1 were available only for fishing years 1964–90 (referred to as 'Murphy').

The second method, that of Doubleday (1976), is referred to as 'separable' VPA. This method assumes that age- and year-specific estimates of F can be partitioned into the product of an age component (partial recruitment) and a year component. The computer program (SVPA.EXE) was developed by Clay (1990) from Pope and Shepherd (1982). This method was applied in two ways to the catch-in-numbers-at-age matrix (or catch matrix) based on annually (not quarterly as in the Murphy VPA, ages 1-4) aged fish. The first approach used the entire catch matrix for 1964-92 (referred to as 'SVPA/All'). Because of large log-catchratio residuals obtained during the early years, the first year in the observed catch matrix was gradually increased from 1964 to 1988, and the approximate coefficient of variation of catch data and sum of squared deviations (output produced by the SVPA.EXE program) were plotted against the initial year of data appearing in the catch matrix (Fig. 3). Because of the rapid drop that occurred in both variables between 1975 and 1976, discrete fits of the separable VPA to the catch matrix for 1964-75 and 1976-92 were also conducted (referred to as 'SVPA/Split').

Results

Historically, ageing gulf menhaden from scales has been problematic, because during certain sampling years only about 50% of the sampled fish showed legible annuli on their scales. The remainder showed no annuli or annuli with odd spacings. These fish were generally assigned ages based on length frequencies and date of capture; moreover, the presence of fish older than age-3 in the population was questioned (Nicholson and Schaaf, 1978). During 1988–89, paired otolith and scale samples were examined from over 500 gulf menha-



Figure 3

Coefficient of variation (CV) of catch data and sum of squared (SSQ) deviations of log catch ratios plotted against increasing starting year of the gulf menhaden, *Brevoortia patronus*, catch matrix used in the separable VPA approach. Starting year varies between 1964 and 1988, and the final year in the catch matrix for all computations is 1992.

den.¹ Results of this study indicated: 1) that by mounting 10 gulf menhaden scales (versus 6 scales under former programmatic guidelines), the chances of the scale reader finding a legible scale were greatly increased; 2) that based on otolith analyses, age-4 gulf menhaden exist in the population; and 3) that assigning ages based on length frequencies was not a useful procedure and therefore was discontinued.

Weighted mean fishing mortalities over ages 1-4 from the three VPA approaches were calculated and were weighted by catch in numbers at age (Fig. 4a). The three values of weighted mean fishing mortality have agreed closely since 1976. However, estimates prior to 1976 varied considerably among the three approaches (Murphy and the two separable VPA's). Prior to 1977 there were few, if any, age-4 fish in the catch matrix. Because convergence was to F at age 2 in the Murphy VPA method, F at older ages was in effect made by forward calculations. Although the forward calculations can diverge from "true" values, when averaged across ages 1-4, they show less year-to-year variability than comparable estimates of F from the separable VPA's. Although the assumptions embedded in Equation 1 may tend to smooth year-to-year variability in the Murphy

Table 3

Estimated convergent *F*, age of convergent *F*, and ages used in Murphy-type virtual population analysis (VPA) for gulf menhaden, *Brevoortia patronus*, by year classes, 1960–89.

| Year | Convergent | Age of | VPA ages | |
|-------|------------|-------------|-------------|--|
| class | F^{I} | convergence | | |
| 1960 | 2.90^{2} | 4 | 4 | |
| 1961 | 1.69^{3} | 3 | 3-4 | |
| 1962 | 1.83 | 2 | 2-4 | |
| 1963 | 2.36 | 2 | 1-3 | |
| 1964 | 3.10 | 2 | 0-4 | |
| 1965 | 1.10 | 2 | 0-3 | |
| 1966 | 2.35 | 2 | 0-3 | |
| 1967 | 2.47 | 2 | 0-4 | |
| 1968 | 1.43 | 2 | 0-4 | |
| 1969 | 1.99 | 2 | 0-4 | |
| 1970 | 1.76 | 2 | 0-3 | |
| 1971 | 1.83 | 2 | 0-4 | |
| 1972 | 3.56^{4} | 3 | 0-3 | |
| 1973 | 0.89 | 2 | 0-4 | |
| 1974 | 1.42 | 2 | 0-4 | |
| 1975 | 2.13 | 2 | 0-4 | |
| 1976 | 1.00 | 2 | 1-4 | |
| 1977 | 0.79 | 2 | 1-4 | |
| 1978 | 1.19 | 2 | 1-4 | |
| 1979 | 1.95 | 2 | 1-4 | |
| 1980 | 1.05 | 2 | 0-4 | |
| 1981 | 1.06 | 2 | 1-4 | |
| 1982 | 1.22 | 2 | 1-4 | |
| 1983 | 1.59 | 2 | 1-4 | |
| 1984 | 1.44 | 2 | 1-4 | |
| 1985 | 2.21 | 2 | 1-4 | |
| 1986 | 2.75 | 2 | 1-4 | |
| 1987 | 1.32 | 2 | 1-4 | |
| 1988 | 0.93 | 2 | 1-4 | |
| 1989 | 1.29 | 2 | 1-3 | |

¹ Convergent F calculated from:

 $F = \ln(C_i) - \ln(C_{i+1}) - M,$

where i = age of convergence and M is the instantaneous natural mortality rate (1.1 yr⁻¹).

² Convergent F for 1960 year class was obtained from the mean F for age-4 fish for year classes, 1964–79.

⁴ Convergent *F* for 1972 year class was obtained from the mean *F* for age-3 fish for year classes 1971 and 1973.

VPA method, estimated weighted mean F for all VPA methods agrees closely for 1976–92 (Fig. 4). This suggests that the separable VPA's, in minimizing log-catch ratio residuals for ages 3 and 4 where ageing errors may be greatest, more profoundly effect resultant fishing mortality estimates at the younger, more critical ages than the Murphy VPA method.

An estimate for natural mortality (M) of 1.1 yr⁻¹ has been used in previous assessments (Nelson and

¹ Smith, J. W., and E. J. Levi. Ageing gulf menhaden, *Brevoortia patronus*, using sagittal otoliths, with a critique of scale reading criteria for the species. NMFS, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516, unpubl. manuscr., 12 p.

³ Convergent F for 1961 year class was obtained from the mean F for age-3 fish for year classes 1964–79.



Figure 4

Mean fishing mortality (*F*) over ages 1–4 for gulf menhaden, *Brevoortia patronus*, compared by method (a: Murphy, SVPA/All, and SVPA/Split) and by natural mortality (b: 0.7, 0.9, and 1.1 yr⁻¹), 1964–92.

Ahrenholz, 1986; Vaughan, 1987). However, estimates of M are often difficult to obtain with precision. Ahrenholz (1981) obtained a range of estimates between 0.7 and 1.6 from tagging studies. Life history approaches suggest estimates of M in the lower part of this range. The method of Hoenig $(1983)^2$ is based on maximum age in the unfished stock, yielding estimates of M ranging from 0.7 for a maximum age of 6 to 1.1for a maximum age of 4. The maximum age of gulf menhaden, found by using otoliths from about 500 fish, was 4 years, suggesting 1.1 as an upper bound on M. Similarly, the method of Pauly (1979),³ which uses estimates of L_{∞} (the maximum asymptotic length) and K (the growth rate parameter) (see next section) and mean temperature (23° to 30°C), suggests a range in Mof 0.9 to 1.1. The lower temperature (23°C) is approximately that when fishing begins in the spring and ends in the fall; while avoidance of temperatures above 30°C has been previously noted (Lassuy, 1983). However, life

history approaches for estimating M do not reflect additional mortality due to other sources (e.g. losses to a small bait fishery or as bycatch in other fisheries). Hence, most analyses that follow assume M equals 1.1.

To investigate sensitivity of fishing mortality estimates to assumed values of natural mortality, additional estimates of fishing mortality were made using the separable VPA on the entire catch matrix (SVPA/All) with lower estimates of M (0.7 and 0.9). Estimates of annual weighted mean F are compared between estimates of Mfor 0.7, 0.9, and 1.1 from SVPA on the entire catch matrix (Fig. 4b). As M is decreased, consistently higher estimates of annual weighted mean F are obtained. Although differences do not appear large, they are not insignificant, especially if the present value of M is a gross overestimate (<< 0.7 compared to 1.1).

Weighted mean fishing mortality from the Murphy VPA ranged between 0.4 in 1981 and 1.5 in 1966. Similarly, weighted mean fishing mortality from the separable VPA's ranged from 0.3 in 1981 to 1.9 in 1975 (all data) and from 0.4 in 1981 to 2.7 in 1975 (split data). Weighted mean fishing mortality rates were highest in the 1960's and declined during subsequent decades (Table 4).

For comparison with and as a continuation of Vaughan (1987), exploitation rates u [proportion re-

 $^{^2}$ ln $M\!=\!1.46-1.01\ln(t_{\rm max}),$ where $t_{\rm max}$ is maximum age in unfished stock.

³ Log₁₀ $M = 0.0066 - 0.279 \log_{10} L_{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T$, where L_{∞} is total length in cm and K in yr⁻¹ are from the von Bertalanffy growth equation, and T is mean water temperature (Celsius).

Decadal and overall averages and range of weighted mean fishing mortality rates (*F*, ages 1–4) for gulf menhaden, *Brevoortia patronus*, 1964–92.

| | | Separable | | | |
|---------|------------|------------|------------|--|--|
| Period | Murphy | All | Split | | |
| 1960's | 1.1 | 1.4 | 1.2 | | |
| 1970's | 0.8 | 1.1 | 1.0 | | |
| 1980's | 0.8 | 0.7 | 0.8 | | |
| 1990's | 0.6 | 0.5 | 0.6 | | |
| Overall | 0.9 | 0.9 | 0.9 | | |
| Range | 0.4 (1981) | 0.3 (1981) | 0.4 (1981) | | |
| | 1.5 (1966) | 2.7 (1975) | 2.5 (1975) | | |

moved annually: $u = F(1-e^{-Z})/Z$, where Z is the total instantaneous mortality rate (M+F)] for ages 1, 2, and 3, and ages 1–4 combined are plotted against year based on the Murphy VPA (Fig. 5). Exploitation rates for age-1 fish have generally declined since 1964, although this trend is less obvious in the exploitation rates for ages 1– 4 combined. Exploitation rates for age-1 fish ranged between 14% in 1986 and 45% in 1966; rates for age-2 fish ranged between 30% in 1981 and 72% in 1966; and for age-3 fish ranged between 36% in 1976 and 71% in 1966. Overall exploitation rates (ages 1–4) ranged between 21% in 1981 and 54% in 1966.

The pattern of recruitment among the three VPA approaches is similar to that of fishing mortality (Fig. 6). Recruits to age 1 have been only slightly higher from the Murphy VPA than those from the separable VPA's since 1976. The separable VPA approaches suggest recruits to age 1 were much more variable prior to 1976 than the Murphy VPA estimates. As suggested earlier in the discussion of weighted mean fishing mortality rates, increased variability in recruitment estimates from the separable VPA approaches may be due to ageing problems during 1964-75, or reduced variability in recruitment from the Murphy VPA approach may be due to assumptions inherent in Equation 1. Because age-1 menhaden form a large component of the population size, the total population (ages 1-4) shows a similar pattern. Recruitment to age 1 and population biomass were highest on average during the 1980's, regardless of VPA used, although peak recruitment and population biomass estimated from the separable approach peaked in 1974 with 55.8 (all) or 42.1 (split) billion recruits to age 1 and with 2.2 (all) or 1.7 (split) million tons of population biomass.



Figure 5

Gulf menhaden, *Brevoortia patronus*, exploitation rates (*u*) for ages 1, 2, 3, and ages 1–4 combined obtained from the Murphy VPA approach, 1964–92.



Figure 6

Recruits to age-1 gulf menhaden, *Brevoortia patronus*, compared from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

Size at Age and Growth Analysis

Interpolated lengths and weights of gulf menhaden at age are needed for estimating optimum fishing yield and spawning stock biomass. Estimates of annual mean weight at age for gulf menhaden in the purse-seine catches were calculated to determine any trends in yield per recruit that could be expected in the fishery. No specific upward or downward trends in mean weight at age are noted (Fig. 7).



Figure 7

Gulf menhaden, *Brevoortia patronus*, mean weight at age, 1964–92.

Weight (in g) is estimated from the weight-length relationship expressed in the linear form of the power function,

$$\ln W = \ln a + b \ln L, \tag{2}$$

where *L* is fork length (mm), and ln *a* and *b* are parameters estimated by linear regression for each fishing year (Table 5). Decadal and overall means of the parameters were calculated across corresponding years with only small differences between decadal means (Table 5). A correction factor ($\sigma^2/2$), where σ^2 is the variance, based on the mean squared error (MSE = 0.01) was used when retransforming from ln *W* to *W* based on properties of the lognormal distribution (Beauchamp and Olson, 1973).

Fork length (L, in mm) can be estimated from age (t, in yr) on the basis of the von Bertalanffy (1938) growth equation,

$$L_{t} = L_{\infty} (1 - e^{-K(t - t_{0})}), \qquad (3)$$

where L_{∞} , K, and t_0 are parameters that in this case were estimated by nonlinear regression (PROC NLIN, Marquardt Option, SAS Institute Inc., 1987). The maximum length (L_{∞}) is approached asymptotically, at a rate described by parameter K, with t_0 (the theoretical length at age-0) shifting the curve to the left or right. For earlier data (1964–79), annual parameter estimates were based on mean length at age (calculated quarterly) (Table 6). For more recent data (1980–92), annual estimates were based on all individual fish weighted by the inverse of numbers at age to improve convergence and correct for parameter bias and poor preci-



Figure 8

Gulf menhaden, *Brevoortia patronus*, mean length at age and corresponding von Bertalanffy growth curve for 1990–92 fishing years.

sion resulting from too few older fish compared with large numbers of young fish noted in Vaughan and Kanciruk (1982). More confidence should be placed in parameters estimated for the more recent years (1980-92). Mean fork length in quarterly age increments for 1990-92 is compared to the von Bertalanffy growth curve fitted to 1990-92 annual quarterly mean lengths (Fig. 8). The nonlinear regression failed to converge for data from four fishing years (1969, 1976-78), so any biological interpretations from the parameter estimates are not valid, although these parameter fits permit interpolation of length at age. Converged estimates of L_{∞} ranged from 224.0 mm to 462.7 mm in fork length, with most annual estimates between 230 and 260 mm. Converged estimates of K ranged from 0.12 yr⁻¹to 0.72 yr⁻¹, with most annual estimates between 0.3 yr⁻¹ and 0.6 yr⁻¹. One should note that because of the typically high correlations among the parameters, ranges in estimates of L_{m} and K can give an exaggerated impression of their variability.

Biological Reference Points for Fishing Mortality

Two modeling approaches are used to estimate biological reference points to assess whether estimated fishing mortality rates are too high. Reference points from the first modeling approach (yield-per-recruit analysis) have been used for several decades, whereas those from the second modeling approach (spawning-stock-biomassper-recruit) have been used recently by the fishery management councils and commissions.

Weight-length regression parameters (and standard errors) for gulf menhaden, *Brevoortia patronus*, by fishing year, 1964–92 (ln $W = \ln a + b \ln L$). Sample size (*n*) and mean squared error (MSE) are also given. Decadal and overall parameters estimates are weighted means (by annual catch in numbers) of parameters from corresponding years.

| Fishing | | | | | |
|---------|--------|--------------|-------------|-------|-------|
| year | n | ln a | b | r^2 | MSE |
| 1964 | 12,420 | -12.6 (0.04) | 3.3 (0.007) | 0.94 | 0.010 |
| 1965 | 15,768 | -12.5(0.03) | 3.3 (0.005) | 0.97 | 0.009 |
| 1966 | 12,830 | -11.5(0.03) | 3.1 (0.006) | 0.95 | 0.007 |
| 1967 | 14,450 | -11.3(0.03) | 3.1 (0.006) | 0.94 | 0.008 |
| 1968 | 15,939 | -11.6(0.03) | 3.2 (0.006) | 0.95 | 0.008 |
| 1969 | 15,076 | -11.4(0.03) | 3.1 (0.006) | 0.95 | 0.009 |
| 1970 | 10,544 | -11.9(0.04) | 3.2 (0.007) | 0.95 | 0.006 |
| 1971 | 7,848 | -12.2(0.04) | 3.3 (0.009) | 0.95 | 0.008 |
| 1972 | 10,025 | -11.7(0.04) | 3.2 (0.008) | 0.94 | 0.008 |
| 1973 | 8,954 | -11.7(0.05) | 3.2 (0.009) | 0.94 | 0.008 |
| 1974 | 10,115 | -10.8(0.04) | 3.0 (0.009) | 0.92 | 0.010 |
| 1975 | 9,528 | -11.6(0.03) | 3.1 (0.007) | 0.96 | 0.008 |
| 1976 | 13,572 | -10.8(0.03) | 3.0 (0.006) | 0.95 | 0.008 |
| 1977 | 14,910 | -11.4(0.02) | 3.1 (0.005) | 0.97 | 0.006 |
| 1978 | 12,983 | -12.1(0.03) | 3.2 (0.006) | 0.96 | 0.006 |
| 1979 | 11,618 | -12.2(0.03) | 3.3 (0.005) | 0.97 | 0.005 |
| 1980 | 9,948 | -13.0(0.05) | 3.4 (0.010) | 0.92 | 0.023 |
| 1981 | 10,405 | -11.7(0.03) | 3.2 (0.006) | 0.96 | 0.010 |
| 1982 | 10,678 | -12.7(0.04) | 3.4 (0.007) | 0.95 | 0.011 |
| 1983 | 14,837 | -12.3(0.03) | 3.3 (0.005) | 0.96 | 0.008 |
| 1984 | 15,955 | -11.9 (0.03) | 3.2 (0.005) | 0.96 | 0.007 |
| 1985 | 13,227 | -11.5(0.03) | 3.1 (0.006) | 0.95 | 0.007 |
| 1986 | 16,495 | -11.8(0.02) | 3.2 (0.005) | 0.97 | 0.006 |
| 1987 | 16,458 | -11.7(0.03) | 3.2 (0.005) | 0.96 | 0.006 |
| 1988 | 12,403 | -11.4(0.04) | 3.1 (0.008) | 0.93 | 0.011 |
| 1989 | 13,951 | -11.8(0.03) | 3.2 (0.007) | 0.95 | 0.007 |
| 1990 | 11,500 | -11.7(0.04) | 3.2 (0.007) | 0.95 | 0.012 |
| 1991 | 11,637 | -12.2(0.04) | 3.3 (0.009) | 0.93 | 0.008 |
| 1992 | 15,231 | -10.4 (0.03) | 2.9 (0.006) | 0.94 | 0.009 |
| 1960's | | -11.8 | 3.2 | | 0.009 |
| 1970's | | -11.7 | 3.2 | _ | 0.007 |
| 1980's | | -11.9 | 3.2 | | 0.009 |
| 1990's | _ | -11.5 | 3.1 | | 0.010 |
| Overall | — | -11.8 | 3.2 | _ | 0.008 |

Yield-per-Recruit Analysis—The trade off between decreasing numbers of fish and increasing biomass per average individual fish forms the conceptual basis for yield-per-recruit analysis. The Ricker (1975; Eq. 10.4) formulation was used for estimating yield per recruit (this was the basis for MAREA used in previous gulf menhaden stock assessments [Nelson and Ahrenholz, 1986; Vaughan, 1987]). Required data include age-specific estimates of fishing mortality (from VPA) and weight (relationships given in Tables 5 and 6). Yield per recruit for gulf menhaden was estimated from estimates of fishing mortality for the three VPA approaches for 1964–92 (Fig. 9).

Two important biological reference points are typically obtained from this approach: F_{max} and $F_{0.1}$. F_{max}

represents the level of fishing mortality which maximizes yield per recruit, while the latter represents the level of fishing mortality where the slope of the increasing yield-per-recruit curve is 10% of the slope at the origin (Sissenwine and Shepherd, 1987). $F_{0.1}$ was developed because it is more conservative than the former, so as to protect against possible recruitment overfishing. Estimates of F_{max} were not obtained for the gulf menhaden data because yield per recruit continues to rise with increasing F (>4.0 yr⁻¹). Estimates of $F_{0.1}$ range between 0.7 (separable VPA approach) and 0.9 (Murphy VPA approach) (Table 7).

Annual estimates of yield per recruit ranged between 20 and 40 g with values generally lower since the late

Estimated von Bertalanffy growth parameters (and asymptotic standard errors) for gulf menhaden, *Brevoortia patronus*, obtained from quarterly mean lengths for fishing years, 1964–92. Estimates (and sample sizes, *n*) are based on quarterly mean lengths for 1964–79 and individual lengths for 1980–92, for use in estimating weight and egg production from spawners. Decadal and overall parameter estimates are from quarterly mean lengths at age for corresponding years. Note that asymptotic standard errors for parameter estimates based on mean lengths are not given.

| Year | n | L_{∞} | K | t_0 |
|---------------------------|------------------------------|-------------------------|--------------|---------------|
| 1964 | 12 | 256.2 | 0.30 | -1.51 |
| 1965 | 13 | 324.9 | 0.20 | -1.53 |
| 1966 | 9 | 269.4 | 0.30 | -1.28 |
| 1967 | 9 | 230.8 | 0.53 | -0.48 |
| 1968 | 12 | 434.2 | 0.12 | -2.26 |
| 19691 | 10 | 753.8 | 0.06 | -2.45 |
| 1970 | 9 | 227.9 | 0.53 | -0.68 |
| 1971 | 10 | 262.7 | 0.33 | -1.20 |
| 1972 | 11 | 227.8 | 0.57 | -0.52 |
| 1973 | 13 | 315.3 | 0.22 | -1.62 |
| 1974 | 9 | 229.0 | 0.72 | -0.20 |
| 1975 | 12 | 462.7 | 0.12 | -2.00 |
| 1976 ¹ | 8 | 493.6 | 0.11 | -1.97 |
| 1977 ¹ | 11 | 508.8 | 0.09 | -2.12 |
| 1978 ¹ | 11 | 427.1 | 0.11 | -2.43 |
| 1979 | 11 | 235.1 | 0.45 | -0.89 |
| 1980 | 9,883 | 232.1 (0.45) | 0.61 (0.006) | -0.04(0.009) |
| 1981 | 10,273 | 241.0 (0.67) | 0.41(0.007) | -0.67(0.032) |
| 1982 | 10,341 | 263.3 (0.99) | 0.29 (0.005) | -1.29(0.037) |
| 1983 | 14,523 | 245.9 (0.75) | 0.40 (0.006) | -0.85(0.031) |
| 1984 | 15,936 | 241.9 (0.52) | 0.44 (0.005) | -0.54(0.021) |
| 1985 | 13,225 | 233.7 (0.65) | 0.51 (0.008) | -0.37(0.022) |
| 1986 | 16,494 | 227.7 (0.43) | 0.54 (0.006) | -0.18(0.018) |
| 1987 | 16,458 | 262.9 (2.23) | 0.27 (0.007) | -1.47(0.049) |
| 1988 | 12,402 | 224.0 (0.78) | 0.51 (0.010) | -0.41 (0.029) |
| 1989 | 13,950 | 241.1 (1.17) | 0.37 (0.008) | -0.94(0.035) |
| 1990 | 11,456 | 234.4 (0.43) | 0.44 (0.006) | -0.67(0.026) |
| 1991 | 11,378 | 234.4 (0.73) | 0.42 (0.008) | -1.06(0.043) |
| 1992 | 14,214 | 235.0 (0.43) | 0.44 (0.006) | -0.87 (0.029) |
| 1960's | 65 | 296.2 | 0.24 | -1.47 |
| 1970's | 102 | 263.9 | 0.35 | -1.01 |
| 1980's | 129 | 242.0 | 0.40 | -0.75 |
| 1990's | 42 | 240.4 | 0.37 | -1.21 |
| Overall | 341 | 244.6 | 0.40 | -0.92 |
| ¹ SAS PROC NLI | N failed to converge, useful | for interpolation only. | | |

1970's (Fig. 9). Yield per recruit, based on estimates of F using the Murphy VPA declined from an average of 32 g during the 1960's to 30 g during the 1970's and 23 g during the 1980's. A value of 26 g was estimated for the 1990 fishing year. Similar decadal mean values were obtained for yield per recruit from estimates of F using the two separable VPA's.

Maximum Spawning Potential—Gabriel et al. (1989) referred to the percent maximum spawning potential (%MSP) as the ratio of spawning stock biomass per

recruit with and without fishing mortality. Hence, the equilibrium spawning stock with an estimated level of fishing mortality is compared to a maximum potential spawning stock as if no fishing had occurred (ignoring adjustments to population parameters through compensatory mechanisms).

Percent maximum spawning potential was calculated in two ways. The first method, described by Gabriel et al. (1989), accumulates female spawning stock biomass per recruit across all ages. The second method accumulates the corresponding number of eggs produced by



Figure 9

Yield per recruit for gulf menhaden, *Brevoortia patronus*, from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

the female biomass, using the relationship of Lewis and Roithmayr (1981).

Values of %MSP below 20 or 30 are typically considered evidence of recruitment overfishing for many Exclusive Economic Zone species (Mace and Sissenwine, 1993). Levels of fishing mortality (with M = 1.1) that produce 20 or 30 %MSP are summarized in Table 7. Estimates of fishing mortality from additional runs of the separable VPA on the complete catch matrix (all data) using lower estimates of natural mortality (M = 0.7 and 0.9) were used to estimate the same biological reference points. A maturation schedule of 0% for ages 0 and 1 and 100% for ages 2 and older was used for gulf menhaden (Nelson and Ahrenholz, 1986).

Annual estimates of maximum spawning potential ranged between 20 and 50% with values generally higher since the late 1970's (Fig. 10). Maximum spawning potential (female biomass) based on estimates of F using the Murphy VPA increased from an average of 24% during the 1960's to 38% during the 1970's and 39% during the 1980's. A value of 48% was estimated for the 1990 fishing year. Similar decadal mean values were obtained for maximum spawning potential from estimates of F using the two separable VPA's.

Spawner-Recruit Relationships

An important question in population dynamics and in fisheries management concerns the degree of dependency between spawning stock and the number of subsequent recruits to the stock. If there is no such depen-

Table 7

Biological reference points from yield-per-recruit (Y/R) and maximum-spawning-potential (%MSP) analyses based on different virtual population analyses (Murphy and separable for M = 1.1, and separable for M = 0.7 and 0.9) for gulf menhaden, *Brevoortia patronus*. Differences in estimates of biological reference points from separable VPA between splitting catch matrix into two time periods and using all data were very slight, so only results from separable VPA using all data are presented. The mean fishing mortality rate (ages 1–4) for the most recent three years (Murphy: 1988–90; SVPA: 1990–92) is given for comparison.

| | | Separable | | | | | |
|------------------------------|----------------------------|---------------|---------------|---------------|--|--|--|
| VPA approach | Murphy (<i>M</i> =1.1) | <i>M</i> =0.7 | <i>M</i> =0.9 | <i>M</i> =1.1 | | | |
| Most recent | | | | | | | |
| Mean F | 0.8 | 0.7 | 0.5 | 0.4 | | | |
| Y/R: <i>F</i> _{0.1} | 0.9 | 0.4 | 0.5 | 0.7 | | | |
| %MSP (Biom | ass) | | | | | | |
| F_{20} | 1.6 | 1.0 | 1.4 | 1.7 | | | |
| F_{30}^{20} | 1.0 | 0.6 | 0.9 | 1.1 | | | |
| %MSP (Eggs) |) | | | | | | |
| F_{20} | 2.6 | 2.6 | 2.7 | 2.9 | | | |
| F_{30} | 2.0 | 2.0 | 2.0 | 2.1 | | | |



Figure 10

Percent maximum spawning potential for gulf menhaden, *Brevoortia patronus*, from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

dency except in the extreme (e.g. no spawners implies no recruits), then there is little that a manager can do to control the number of recruits (and hence future stock sizes), other than to assure that there are sufficient spawners to produce subsequent recruits to the population and to preserve the quality of the habitat utilized by the prerecruit juveniles. If there is a quantifiable relationship between spawning stock and recruits, then management can be designed to maximize the landings or some other objective based on this relationship. To investigate the relationship between spawners and recruits, the Ricker (1954) model was used (see arguments by Nelson and Ahrenholz [1986] for a domeshaped spawner-recruit relationship).

Estimation of recruits to age 1 has been described in the VPA section (Fig. 6). Estimation of spawning stock in numbers was estimated as the number of adults (ages 2 through 4 on 1 January). Spawning stock biomass in weight is calculated annually from the above numbers at age multiplied by the weight at age, calculated from the weight-length (Table 5) and length-age (Table 6) relationships. Potential egg production was also estimated as an index of spawners. Estimates of egg production as a function of fish length were obtained from the equation (Lewis and Roithmayr, 1981):

$$\ln (EGGS) = -9.872 + 3.877 \ln L, \tag{4}$$

where *EGGS* equals total numbers of eggs produced per female; *L* equals estimated fork length (mm); n = 70, $s_{y,x} = 0.375$ (root mean squared error); and $r^2 = 0.65$. Expected egg production per female of a given age was calculated using Equation 4 and lengths from Table 6. This is intended more as a relative, rather than absolute, measure of egg production because the possibility of batch spawning is not considered. Assuming a 1:1 sex ratio, spawning stock as potential eggs (*PE*) is calculated by

$$PE = \frac{1}{2} \sum EGGS_i N_i, \tag{5}$$

where $EGGS_i$ is egg production per female at age *i*, and N_i is population numbers at age *i*. Since 1964, the egg production by age-2 spawners has contributed significantly (greater than 70%) to the total spawning egg production (Fig. 11), ranging between 70 and 97% for the Murphy VPA approach and 72 to 99% for the SVPA approaches.

Based on estimated F from the Murphy VPA, spawning biomass was on average highest during the 1980's when it averaged 410,200 t and lowest during the 1960's when it averaged 105,700 t. Intermediate values were obtained during the 1970's when spawning stock biomass averaged 292,200 t, and 334,000 t was estimated for 1990. Estimated mean spawning stock biomass by decade based on estimated F from the separable VPA using all the catch matrix were: 108,000 t (1960's), 234,200 t (1970's), 343,600 t (1980's), and 324,000 t (1990–92). Similarly, estimated mean spawning stock



Figure 11

Percent contribution of age-2 gulf menhaden, *Brevoortia patronus*, egg production to total egg production from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

biomass by decade based on estimated F from the separable VPA which splits the catch matrix were: 102,800 t (1960's), 234,000 t (1970's), 321,600 t (1980's), and 275,400 t (1990–92).

Parameters of the Ricker model were estimated by nonlinear regression (SAS Institute Inc., 1987) from the equation:

$$R = \alpha S \, e^{-\beta S},\tag{6}$$

where *R* equals recruits to age 1, *S* equals spawners (numbers, biomass, or potential egg production), and α and β are parameters to be estimated. Plots of the fitted model overlayed with observed data are compared for the three VPA approaches (Fig. 12).

Although the density-dependent parameter (β) is significantly different from 0 for all three VPA approaches, there is only an 18% improvement in mean squared error from the nonlinear fit of the spawnerrecruit Ricker model for data from the Murphy VPA approach over the variance of the mean number of recruits to age 1 (thereby suggesting that the number of recruits is independent of spawning stock size). The mean squared errors associated with the nonlinear fit of the Ricker model for the two SVPA approaches were actually lower than the corresponding variances of the mean number of recruits to age 1. As illustrated in Figure 12, considerable variability remains due to environmental conditions or measurement error. Given the variability evident from these regressions, their use is of limited value (e.g. not useful for predicting future absolute population sizes). However, the density dependence parameter is significant $(H_0: \beta > 0)$, so that the number of future recruits does depend, albeit weakly, to some extent upon the size of the spawning stock which produced them.

Parameter estimates (and asymptotic standard errors) for the Ricker spawner-recruit model were obtained from estimates of spawning stock biomass and recruits to age 1 from the three VPA approaches (Table 8). Also estimated were the maximum number of recruits and spawning stock biomass that produced them (Ricker, 1975). For the Murphy VPA, mean recruitment during the 1980's (33 billion fish) exceeded the maximum predicted by the Ricker curve by 2 billion recruits to age 1. During that time (1980's), spawning stock biomass averaged 410,200 t (or 34,200 t less than the "optimal" size). The most recent estimate of spawning stock biomass is 334,000 t (in 1990) which is 110,000 t below the estimate of spawning stock biomass giving maximum recruitment. However, because of the large unexplained error remaining from fitting the Ricker curve, the predicted value of 29.6 billion recruits from 334,000 t of spawners has a very large confidence interval (approximate 95% confidence interval is between 10.1 and 49.1 billion recruits to age 1).

Table 8

Parameter estimates (and asymptotic standard error, ASE) for the Ricker spawner-recruit model applied to gulf menhaden, *Brevoortia patronus*, using estimates of the recruits to age 1 (in millions of fish) and spawning stock biomass (in thousands of metric tons) from three VPA approaches. Also estimated are the maximum number of recruits to age 1 and the spawning stock biomass that produces them (Ricker, 1975).

| | | SVPA | | | |
|--|---------|---------|---------|--|--|
| Parameter | Murphy | All | Split | | |
| α | 187.7 | 252.2 | 211.0 | | |
| $ASE(\alpha)$ | 36.2 | 55.7 | 46.3 | | |
| β | 0.00225 | 0.00349 | 0.00311 | | |
| ASE(β) | 0.00051 | 0.00072 | 0.00072 | | |
| Maximum recruits $\alpha/\beta e$ | 30,700 | 26,600 | 25,000 | | |
| Corresponding spawning stock biomass | | | | | |
| $1/\beta$ | 444.4 | 286.5 | 321.5 | | |



Figure 12

Spawner-recruit relations for gulf menhaden, *Brevoortia patronus*, from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

Surplus Production Models

Surplus production models relate historical landings and fishing effort data to obtain estimates of maximum sustainable yield (MSY). Catch per unit effort (CPUE) is assumed proportional to population abundance, and fishing effort is assumed proportional to fishing mortality. Under equilibrium assumptions, plotting landings against effort gives a dome-shaped curve. This does not appear to be the case for gulf menhaden data, although the points may lie along the ascending limb of such a curve (Fig. 13).

Specifically, when relating fishing effort (*E*) to instantaneous fishing mortality rate (*F*), the catchability curve (q) is assumed to be constant i.e.

$$F = qE,\tag{7}$$

where the unit of fishing effort, *E*, is defined as vesselton-weeks for gulf menhaden. As noted in Nelson and Ahrenholz (1986), the above unit of fishing effort, referred to as nominal effort, is not a reliable measure of fishing mortality. A unit of fishing effort that is reliable is referred to as effective effort. The difficulty in directly obtaining a reliable unit of fishing effort results from the schooling nature of clupeid fishes, which are more susceptible to fishing effort than nonschooling species (see discussion of "dynamic aggregation process" in Clark and Mangel [1979]). Severe stock depletion, however, could occur before it was indicated by an analysis of landings and CPUE data.

To demonstrate that the population catchability coefficient, q, for gulf menhaden is not constant but de-



Figure 13

Gulf menhaden, *Brevoortia patronus*, landings plotted against nominal fishing effort, 1946–92.

pendent upon population size, it was estimated by solving Equation 7 for q (= F/E) for each fishing year since 1964 and compared with the population size (ages 1-4) for the same fishing year (Fig. 14; separate estimates based on Murphy and separable VPA's). As noted in Nelson and Ahrenholz (1986), there is a pronounced inverse relationship between the catchability coefficient and population size. The natural logarithm of q was regressed against population size for each VPA (Murphy and two separable: all and split catch matrices). The highest r value (0.74) was obtained using estimates of population size and weighted mean F from the Murphy VPA; lower values of r were obtained from the two separable VPA's (0.43 and 0.52 for all and split catch matrices, respectively). Using the Murphy VPA approach, Equation 7 involves the estimates of F, and so estimates of q will be sensitive to assumptions embedded in Equation 1. However, we believe these effects are minor. Greater effect is likely from the ageing error in the earlier years (1964-75) on the separable VPA estimates of F and hence estimates of q.

To adjust nominal fishing effort to account for variations in q, the 1964 value of $q(q_a)$ was used to adjust nominal effort (*E*) so that q is constant (q_a) i.e.

$$E' = E q/q_a, \tag{8}$$

where E' is a unit of "effective" fishing effort (Fig. 15; separate estimates based on Murphy and separable VPA's). Note that while nominal effort was increasing from 1964 through the mid-1980's, effective fishing effort has remained low.

The computer program PRODFIT (Fox, 1975), which attempts to account for nonequilibrium conditions through a smoothing process, is used to estimate parameters (and MSY) for the Pella-Tomlinson generalized production model (Pella and Tomlinson, 1969):

$$U = (A + BE')^{1/(m-1)},$$
(9)

where U is catch per unit of effort, and A, B, and m are parameters to be estimated. In using PRODFIT, principally two ages are assumed to contribute to the landings (Fig. 2). Parameter estimates and associated square root of the variability index (Fox, 1975) for the three VPA approaches are summarized in Table 9. Estimates of MSY based on 1946-92 fishing years range from 664,000 t based on Murphy VPA, to 708,000 t and 897,000 t based on separable VPA's (all and split data in catch matrix, respectively). The estimated generalized production curves are compared to observed data in Fig. 16. Only with the estimated model based on the separable VPA with split catch matrix would there be significant concern that if effort rose too high, the stock might potentially collapse because of the steepness of the right-hand side of the curve. For this model



Figure 14

Catchability coefficient (q) versus estimated population size for gulf menhaden, *Brevoortia patronus*, from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

Table 9

Parameter estimates for the generalized surplus production model using PRODFIT (Fox, 1975) with nominal fishing effort for 1946–63 and effective fishing effort from 1964–92 applied to gulf menhaden, *Brevoortia patronus*. Square root of variability index is in parentheses beside point estimate.

| | | | | S | VPA | |
|-----------|------|-------------|-------|-----------|---------|---------|
| Parame | eter | ter Murphy | | All | | lit |
| A | 10. | 8 (10.3) | 1.44 | (1.29) | 142.8 (| 453.6) |
| В | -0. | 027 (0.028) | -0.00 | 1 (0.003) | -0.232 | (0.744) |
| m | 2 | 46 (0.71) | 1.17 | (0.43) | 6.66 | (4.08) |
| MSY | 664. | 1 (57.0) | 708.1 | (64.5) | 897.4 (| 136.6) |
| f_{MSY} | 241 | 5 (25.9) | 209.7 | (29.1) | 522.2 | (44.2) |

m was estimated as 1.2. An *m* of 2.5 was obtained for the Murphy VPA, and 6.6 for the SVPA (all).

Variability associated with all model parameters (*A*, *B*, and *m*) was large, and corresponding comparisons of data to model fits show considerable lack of fit (as noted in Vaughan [1987] to which these estimates can be compared). Usefulness of these models beyond suggesting order-of-magnitude level of MSY is debatable.



Figure 15

Gulf menhaden, *Brevoortia patronus*, nominal and effective fishing effort from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1946–92.

However, because gulf menhaden are a short-lived species with few ages contributing to the landings, surplus production models are probably of greater use than for long-lived species, with many ages contributing to the landings. However, other methods are available which more adequately address the problem of nonequilibrium conditions (e.g., GENPROD).

Conclusions

The gulf menhaden fishery is conducted within the territorial sea and offshore of five coastal states (Florida to Texas). All states, except Florida, enacted the cooperative management plan under the Gulf States Marine Fisheries Commission (GSMFC) in 1977 (Christmas and Etzold, 1977). The plan was revised in 1983 and 1988 (Christmas et al., 1983, 1988) and was under revision during 1993. Because management authority is vested in the individual states, some regulations are area-specific to a state or county, but other regulations, such as length of fishing season (mid-April through mid-October), are common to all states, except Florida. A proposal to extend the fishing season through 1 November was adopted by the GSMFC at their March 1993 annual meeting. No state, however, controls or limits the catch or fishing effort of vessels.

Landings and nominal effort were quite high during the 1980's but declined precipitously during the late 1980's and early 1990's. Landings peaked in 1984 with 982,800 t, while nominal fishing effort peaked in 1983 with 655,800 vessel-ton-weeks. Most recently (1992), landings were 421,400 t with 408,000 vessel-ton-weeks. Landings between 1982 and 1987 were very high, exceeding estimates of long-term MSY, but were supported by generally high recruitment to age 1. More recent landings (421,400 to 623,700 t) are comparable to, or somewhat below, recent estimates of MSY (600,000 to 700,000 t based on the generalized production model for the Murphy VPA results). Vaughan (1987) noted an upward trend in historical estimates of MSY, which were not found in this assessment.

The quality of the catch matrix for fishing years 1964– 76 is questioned as a result of the information presented in Figure 3. The number of age-4+ menhaden during this early period is probably underestimated. Numbers of fish in the landings for all ages (except age 0) were higher during the peak landings of the mid-1980's than earlier during the 1960's and 1970's. Fishing mortality appears to have been slightly higher (and %MSP slightly lower) during this early period (1964– 75) when the lack of age-4+ menhaden in the catch matrix contributed to highly variable estimates of *F* from the SVPA (Figs. 4 and 10). The Murphy VPA estimates of *F* (and %MSP) are more stable during this early period, as



Figure 16

Surplus production models for gulf menhaden, *Brevoortia patronus*, from three VPA approaches (Murphy, SVPA/All, and SVPA/Split), 1964–92.

noted earlier, because the analysis hinges on the slope between the catch of age-2 and age-3 menhaden (see Eq. 1). All three VPA approaches produce very similar results (*F* and recruits to age 1) for the period 1976–92.

Recent estimates of recruits to age 1 are still reasonable (20 to 25 billion). Spawning stock biomass for recent years is on average well above that of the 1960's and higher than that of the 1970's regardless of VPA approach.

Recent estimates of fishing mortality (for M = 1.1) compare favorably with the different estimates of biological reference points. Generally, estimates of $F_{0.1}$ are similar to (but slightly smaller than) estimates of F_{30} , but are much smaller than estimates of F_{20} . Recent estimates of F (ages 1–4) are comparable to or below $F_{0.1}$, the most conservative of the above biological reference points.

When lower estimates of natural mortality (*M*) are assumed, then the estimated biological reference points decrease while estimates of fishing mortality increase. For *M* of 0.9, recent estimates of *F* (mean of 0.5 for 1990–92) are about the same as for $F_{0.1}$ (0.5), and well below estimates of F_{20} (1.4–2.7) and F_{30} (0.9–2.0). Only when *M* is assumed even lower (0.7), do recent estimates of *F* (mean of 0.7 for 1990–92) fall above $F_{0.1}$ (0.4), although the mean is still generally below estimates of F_{20} (1.0–2.6) and F_{30} (0.6–2.0). We still consider *M* equal to 1.1, based on tagging, as the best point estimate.

In summary, the gulf menhaden has higher natural mortality and is shorter lived than the Atlantic menhaden, which can result in rapid annual changes in fishable stock. The gulf menhaden fishery is currently fully exploited and the population appears reasonably stable in view of the age composition, life span, and effects of environmental factors. Annual production, fishing effort, and fleet size appear reasonably balanced and risk of overfishing relatively low with the 1992–93 fleet size and recent mean recruitment. Given the variability in the data and model estimates, recent landings below long term MSY (and well below high landings of the mid-1980's) do not suggest that the stock is in trouble.

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