NOAA Technical Report NMFS 58

September 1987

Stock Assessment of the Gulf Menhaden, *Brevoortia patronus*, Fishery

Douglas S. Vaughan

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA TECHNICAL REPORT NMFS

The major responsibilities of the National Marine Fisheries Service (NMFS) are to monitor and assess the abundance and geographic distribution of fishery resources, to understand and predict fluctuations in the quantity and distribution of these resources, and to establish levels for their optimum use. NMFS is also charged with the development and implementation of policies for managing national fishing grounds, development and enforcement of domestic fisheries regulations, surveillance of foreign fishing off United States coastal waters, and the development and enforcement of international fishery agreements and policies. NMFS also assists the fishing industry through marketing service and economic analysis programs, and mortgage insurance and vessel construction subsidies. It collects, analyzes, and publishes statistics on various phases of the industry.

The NOAA Technical Report NMFS series was established in 1983 to replace two subcategories of the Technical Reports series: "Special Scientific Report—Fisheries" and "Circular." The series contains the following types of reports: Scientific investigations that document long-term continuing programs of NMFS; intensive scientific reports on studies of restricted scope; papers on applied fishery problems; technical reports of general interest intended to aid conservation and management; reports that review in considerable detail and at a high technical level certain broad areas of research; and technical papers originating in economics studies and from management investigations. Since this is a formal series, all submitted papers receive peer review and those accepted receive professional editing before publication.

Copies of NOAA Technical Reports NMFS are available free in limited numbers to governmental agencies, both Federal and State. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies may be obtained from: U.S. Department of Commerce, National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161. Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

13. Guidelines for reducing porpoise mortality in tuna purse seining, by James M. Coe, David B. Holts, and Richard W. Butler. September 1984, 16 p.

14. Synopsis of biological data on shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818, by Michael J. Dadswell, Bruce D. Taubert, Thomas S. Squiers, Donald Marchette, and Jack Buckley. October 1984, 45 p.

15. Chaetognatha of the Caribbean sea and adjacent areas, by Harding B. Michel. October 1984, 33 p.

16. Proceedings of the Ninth and Tenth U.S.-Japan Meetings on Aquaculture, by Carl J. Sindermann (editor). November 1984, 92 p.

17. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean, by Gary A. Wolff. November 1984, 50 p.

18. A temporal and spatial study of invertebrate communities associated with hard-bottom habitats in the South Atlantic Bight, by E. L. Wenner, P. Hinde, D. M. Knott, and R. F. Van Dolah. November 1984, 104 p.

19. Synopsis of biological data on spottail pinfish, *Diplodus holbrooki* (Pisces: Sparidae), by George H. Darcy. January 1985, 11 p.

20. Ichthyoplankton of the Continental Shelf near Kodiak Island, Alaska, by Arthur W. Kendall, Jr., and Jean R. Dunn. January 1985, 89 p.

21. Annotated bibliography on hypoxia and its effects on marine life, with emphasis on the Gulf of Mexico, by Maurice L. Renaud. February 1985, 9 p.

22. Congrid eels of the eastern Pacific and key to their Leptocephali, by Solomon N. Raju. February 1985, 19 p.

23. Synopsis of biological data on the pinfish, *Lagodon rhomboides* (Pisces:Sparidae), by George H. Darcy. February 1985, 32 p.

24. Temperature conditions in the cold pool 1977-81: A comparison between southern New England and New York transects, by Steven K. Cook. February 1985, 22 p.

25. Parasitology and pathology of marine organisms of the world ocean, by William J. Hargis, Jr. (editor). March 1985, 135 p.

26. Synopsis of biological data on the sand perch, *Diplectrum formosum* (Pisces: Serranidae), by George H. Darcy. March 1985, 21 p.

27. Proceedings of the Eleventh U.S.-Japan Meeting on Aquaculture, Salmon Enhancement, Tokyo, Japan, October 19-20, 1982, by Carl J. Sindermann (editor). March 1985, 102 p.

28. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific, by William F. Perrin, Michael D. Scott, G. Jay Walker, and Virginia L. Cass. March 1985, 28 p.

29. Prevalence, intensity, longevity, and persistence of *Anisakis* sp. larvae and *Lacistorhynchus tenuis* metacestodes in San Francisco striped bass, by Mike Moser, Judy A. Sakanari, Carol A. Reilly, and Jeannette Whipple. April 1985, 4 p.

30. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838, by Sandra E. Shumway, Herbert C. Perkins, Daniel F. Schick, and Alden P. Stickney. May 1985, 57 p.

31. Shark catches from selected fisheries off the U.S. east coast, by Emory D. Anderson, John G. Casey, John J. Hoey, and W. N. Witzell. July 1985, 22 p.

32. Nutrient Distributions for Georges Bank and adjacent waters in 1979, by A. F. J. Draxler, A. Matte, R. Waldhauer, and J. E. O'Reilly. July 1985, 34 p.

33. Marine flora and fauna of the Northeastern United States. Echinodermata: Echinoidea, by D. Keith Serafy and F. Julian Fell. September 1985, 27 p.

34. Additions to a revision of the shark genus *Carcharhinus*: Synonymy of *Aprionodon* and *Hypoprion*, and description of a new species of *Carcharhinus* (Carcharhinidae), by J. A. F. Garrick. November 1985, 26 p.

35. Synoptic review of the literature on the Southern oyster drill *Thais haemastoma floridana*, by Philip A. Butler. November 1985, 9 p.

36. An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, by Reuben Lasker (editor). December 1985, 99 p.

37. A histopathologic evaluation of gross lesions excised from commercially important North Atlantic marine fishes, by Robert A. Murchelano, Linda Despres-Patanjo, and John Ziskowski. March 1986, 14 p.

38. Fishery atlas of the northwestern Hawaiian Islands, by Richard N. Uchida and James H. Uchiyama (editors). September 1986, 142 p.

39. Survey of fish protective facilities at water withdrawal sites on the Snake and Columbia Rivers, by George A. Swan, Tommy G. Withrow, and Donn L. Park. April 1986, 34 p.

40. Potential impact of ocean thermal energy conversion (OTEC) on fisheries, by Edward P. Myers, Donald E. Hoss, Walter M. Matsumoto, David S. Peters, Michael P. Seki, Richard N. Uchida, John D. Ditmars, and Robert A. Paddock. June 1986, 33 p.

41. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes, by James A. Bohnsack and Scott P. Bannerot. July 1986, 15 p.

42. Effects of temperature on the biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine, by Spencer Apollonio, David K. Stevenson, and Earl E. Dunton, Jr. September 1986, 22 p.

43. Environment and resources of seamounts in the North Pacific, by Richard N. Uchida, Sigeiti Hayasi, and George W. Boehlert (editors). September 1986, 105 p.

44. Synopsis of biological data on the porgies, *Calamus arctifrons* and *C. proridens* (Pisces: Sparidae), by George H. Darcy. September 1986, 19 p.

45. Meristic variation in *Sebastes* (Scorpaenidae), with an analysis of character association and bilateral pattern and their significance in species separation, by Lo-chai Chen. September 1986, 17 p.

46. Distribution and relative abundance of pelagic nonsalmonid nekton off Oregon and Washington 1979-84, by Richard D. Brodeur and William G. Pearcy. December 1986, 85 p.

NOAA Technical Report NMFS 58

Stock Assessment of the Gulf Menhaden, *Brevoortia patronus*, Fishery

Douglas S. Vaughan

September 1987

U.S. DEPARTMENT OF COMMERCE
C. William Verity, Jr., Secretary
National Oceanic and Atmospheric Administration
Anthony J. Calio, Administrator
National Marine Fisheries Service
William E. Evans, Assistant Administrator for Fisheries

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

CONTENTS

Stock Assessment of the Gulf Menhaden, *Brevoortia patronus*, Fishery

Douglas S. Vaughan
Beaufort Laboratory
Southeast Fisheries Center
National Marine Fisheries Service, NOAA
Beaufort, North Carolina 28516-9722

ABSTRACT

A stock assessment of the gulf menhaden, *Brevoortia patronus*, fishery was conducted with data on purse-seine landings from 1946 to 1985 and port sampling data from 1964 to 1985. These data were analyzed to determine growth rates, yield-per-recruit, spawner-recruit relationships, and maximum sustainable yield (MSY). Virtual population analysis was used to estimate stock size, year-class size, and fishing mortality rates. During the period studied, an average of 27% of age-1 fish and 55% of age-2 and age-3 fish were taken by the fishery, and 54% for age-1 and 38% for age-2 and -3 fish were lost annually to natural causes.

Annual yield-per-recruit estimates ranged from 6.9 to 19.3 g, with recent mean conditions averaging 12.2 g since 1978. Surplus production models produced estimates of MSY from 620 to 700 kilometric tons. Recruits to age-1 ranged from 8.3 to 41.8 billion fish for 1964-82. Although there was substantial scatter about the fitted curves, Ricker-type spawner-recruit relationships were found suitable for use in a population simulation model. Estimates of MSY from population simulation model runs ranged from 705 to 825 kilometric tons with *F*-multiples of the mean rate of fishing ranging from 1.0 to 1.5.

Recent harvests in excess of the historical MSY may not be detrimental to the gulf menhaden stock. However, one should not expect long-term harvesting above the historical MSY because of the short life span of gulf menhaden and possible changes from currently favorable environmental conditions supporting high recruitment.

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 (Christmas et al. 1983; Nelson and Ahrenholz 1986). Adult menhaden are filter feeders (feeding primarily on phytoplankton) and, in turn, support predatory food fishes. Gulf menhaden form large surface schools which appear in the nearshore Gulf waters from about April to November. Although no extensive coastwise migrations are known to occur, there is evidence that older fish move towards the Mississippi River delta (Ahrenholz 1981). Spawning occurs in offshore waters during winter, peaking during December and January (Lewis and Roithmayr 1981). Eggs hatch at sea and the larvae are carried to estuaries by ocean currents where they develop into juveniles. 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 purse-seine fishery in the northern Gulf of Mexico (Fig. 1) from mid-April through mid-October as regulated by interstate compact (Christmas and Etzold 1977; Nelson and Ahrenholz 1986). Since 1964 the National Marine Fisheries Service (formerly Bureau of Commercial Fisheries) 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 10 and 14, except in 1985 when it fell to 7 plants (Table 1). The number of purse-seine vessels has varied between 66 and 92, with 73 vessels active during the 1985 fishing season. Annual landings and nominal fishing effort (vessel-ton-week), available since 1946, show an upward trend with record high landings during the 1984 fishing season (Fig. 2). Since 1964 detailed information on daily vessel landings and fish sampled for length, weight, and age (from scales) are available. This information is used to estimate the number of fish landed at age, 1964-85 (Table 2). The fishery depends primarily on age-1 fish (comprising from 47.2% to 92.0% of the landings) and to a lesser extent on age-2 fish (7.3% to 45.2%) (Fig. 3). The remaining ages (age-0, -3, and -4+) generally contribute insignificantly to the landings (0.6% to 12.7%), although age-3 fish contributed 10.2% to the landings in 1975.

Nelson and Ahrenholz (1986) analyzed the gulf menhaden data for the 1964-78 fishing years, and recent landings (700-980 kilometric tons (kmt) since 1975) exceed reported estimates for MSY (540 to 640 kmt). The purpose of this report is to reevaluate the gulf menhaden stock with data included from seven more fishing years. As shown by the catch data (Table 2 and Fig. 3), gulf menhaden are a short-lived species, requiring constant stock monitoring through annual data collection and frequent assessments. The analyses that follow closely parallel those presented in Nelson and Ahrenholz (1986). Estimates of population numbers and fishing mortality rates by age are obtained from virtual population analysis (VPA). Growth in length is obtained by considering mean length-at-age by year class and fitting the von Bertalanffy growth function to these data to obtain parameter estimates; growth in weight is obtained by relating weight to length by fishing year. Yield-per-recruit is obtained for each year class and for two sets of mean conditions (1964-85 fishing years and 1978-85 fishing years). By adjusting nominal fishing effort for variability in the catchability coefficient to obtain estimates of effective effort for 1964-83, parameters for the Schaefer and Pella-Tomlinson surplus production models are estimated from yield and fishing effort data from 1946 to 1985. Estimates of maximum sustainable yield (MSY) are also obtained from these models. Population simulation

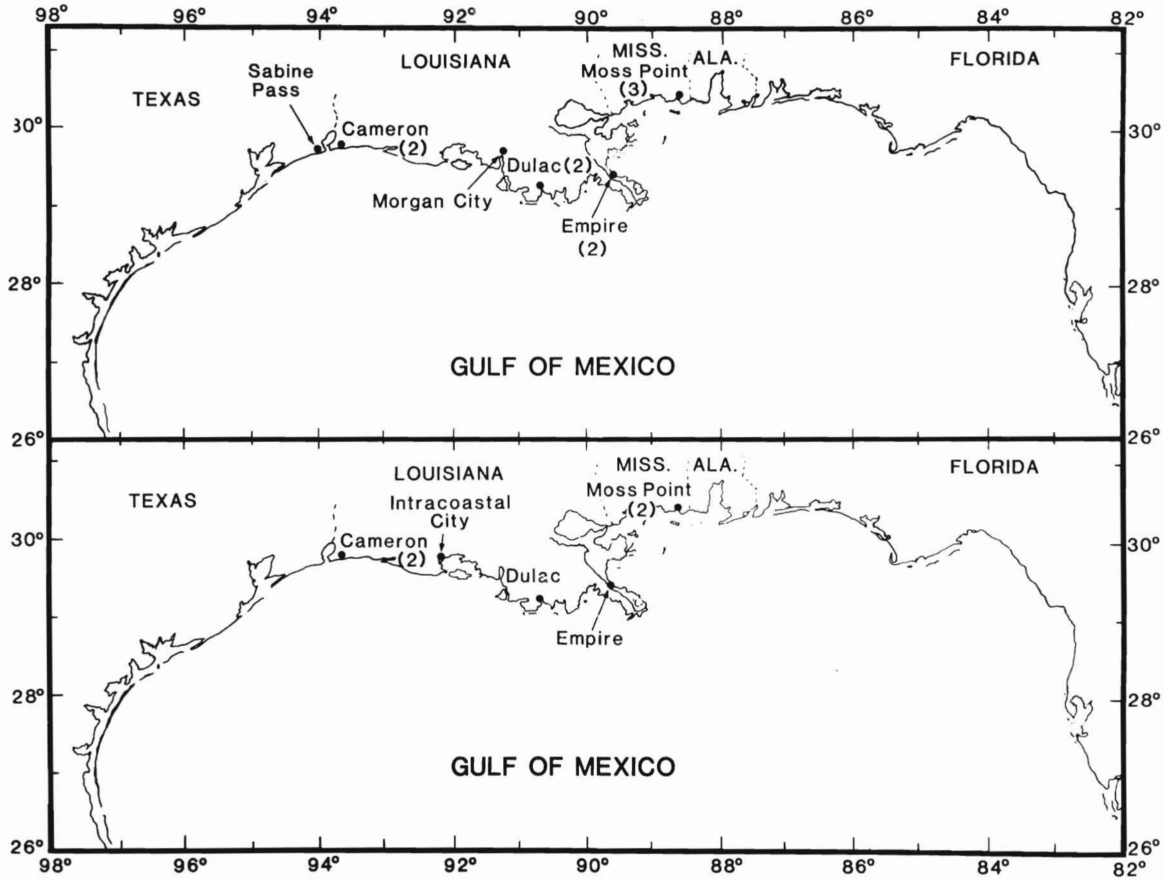

Figure 1
Map of northern Gulf of Mexico showing port locations for active plants in 1964 (upper) and in 1985 (lower).

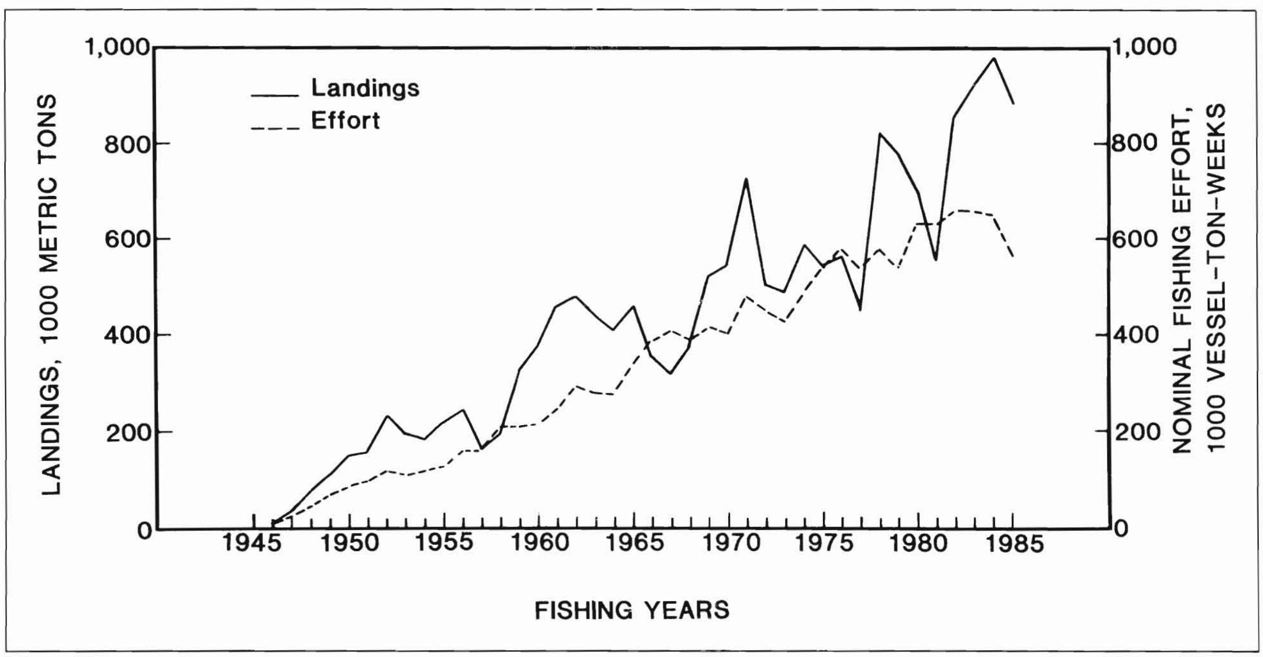

Figure 2
Gulf menhaden landings and nominal fishing effort for fishing years, 1946-85.

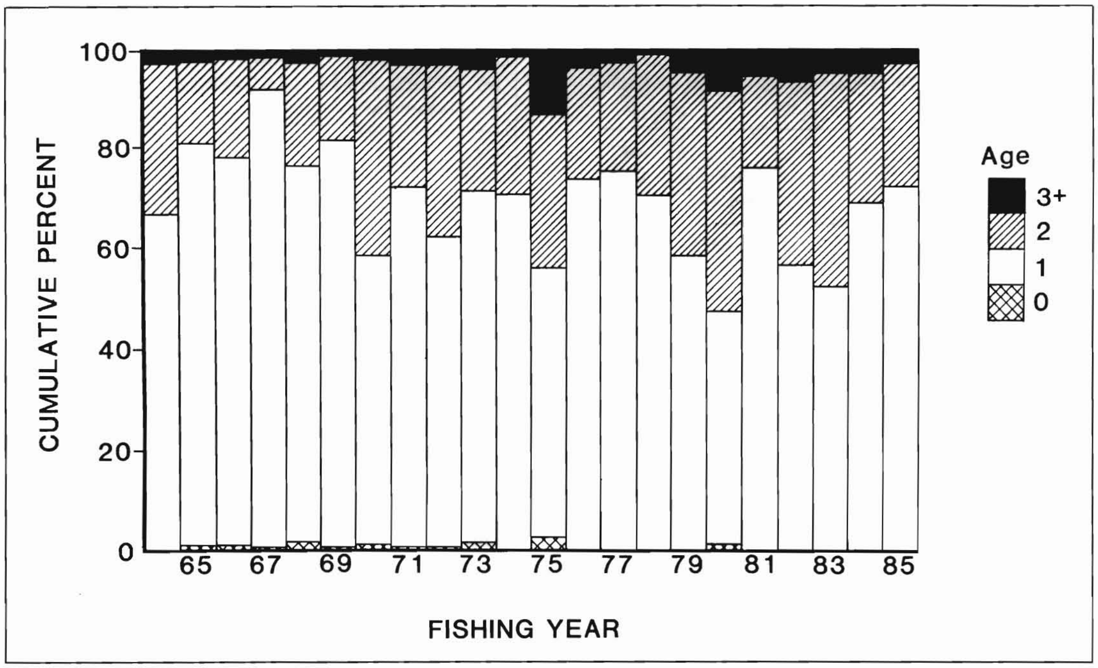

Figure 3
Contribution in percent of total numbers of gulf menhaden landed by age group, 1964-85.

models are used to investigate the equilibrium (sustainable) yields from the gulf menhaden stock when different levels of fishing mortality (F-multiples) are applied, based on two Ricker models (number of recruits on number of spawners and number of recruits on spawners as eggs) and on the assumption of random recruitment. Estimates of MSY are obtained from the population simulation model and compared with those estimates from the surplus production models. The results of the models are used to evaluate the impact of the fishery on the gulf menhaden stock.

Virtual Population Analyses

Estimates of initial population sizes and fishing mortality rates by age are obtained from virtual population analysis (VPA) as developed by Murphy (1965) and modified by Tomlinson (1970). Tomlinson's computer program MURPHY (Abramson 1971) was used for these calculations, which are independent of catch-per-unit-effort (CPUE). Backward sequential computations (oldest to youngest age) were used because they tend to converge on the same estimates, while forward calculations tend to diverge unless the true starting value was used.

A major component of the input data for this analysis is catch in numbers-at-age. 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. The catches in numbers-at-age were summarized by quarter from weekly estimates by sampling methods outlined by Nicholson (1978) and reviewed in Chester (1984). The annual instantaneous natural mortality rate (M) was obtained from an analysis of mark-recapture data (Ahrenholz 1981). 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 aging, especially with 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. Estimates of the annual instantaneous fishing mortality rate (F_i) for age-2 fish were derived separately for each year class primarily from comparing catches of age-2 and age-3 fish,

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

where C is the annual catch in numbers-at-age (i or $i+1$). Following Nelson and Ahrenholz (1986), initial starting values of F for the oldest age group landed in a year class were adjusted by trial and error until the sum of the quarterly F's for age-2 fish was virtually equal to the annual estimate of F_2 obtained from Eq. (1) (Table 3). Since an extremely low value of F_2 was obtained for the 1972 year class, and a negative value of F_2 was obtained for the 1979 year class, a convergence criterion based on F for age-3 fish was used instead. Since no age-4 fish were landed from the 1972 year class, an average of F for age-3 fish from the 1971 and 1973 year classes was used. Furthermore, no age-2 fish were available in the landings data for the 1960 and 1961 year classes (sampling began in 1964), and no age-3 fish were available in the landing data for the 1960 year class. The mean F for age-3 fish for year classes 1964 through 1979 was used for estimating F for age-3 fish in the 1961 year class, and the mean F for age-4 fish for year classes 1964 through 1979 was used for estimating F for age-4 fish in the 1960 year class.

The distribution of numbers-at-age in the population as estimated from the VPA for years 1964-80 on 1 January (beginning of the first quarter, Table 4) closely parallel the distribution of numbers-at-age in the landings (Table 2) for the same years. Recruits at age-1 on 1 January ranged from 8.3 billion fish in 1966 to 41.8 billion fish in 1982, with the three highest recruitment years for the study period (1964-80) being the 1978, 1981, and

Table 1

Number of gulf menhaden reduction plants by port and total, number of purse-seine vessels, and number of fish sampled for age and size for fishing years, 1964-85.

Fishing year	Ports								No. reduction plants	No. reduction vessels	No. fish sampled
	A	MP	E	D	MC	IC	C	SP			
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	16,000
1985	0	2	1	1	0	1	2	0	7	73	13,240

A = Appalachicola, FL: Fish Meal Co. (1966, 1968-69).
MP = Moss Point, MS: Seacoast Products Co. (1964-72, 1975-84), Standard Products Co. (1964-85), Zapata Haynie, Inc. (1964-85).
E = Empire, LA: Empire Menhaden Co. (1964-85), Petrou Fisheries, Inc. (1964-84).
D = Dulac, LA: Dulac Menhaden Fisheries (1964-1968, 1970-71), Fish Meal and Oil Co. (1964-65), Zapata Haynie, Inc. (1965-85).
MC = Morgan City, LA: Seacoast Products Co. (1964-84).
IC = Intracoastal City, LA: Seacoast Products Co. (1965-84), Zapata Haynie, Inc. (1985).
C = Cameron, LA: Louisiana Menhaden Co. (1964-85), Seacoast Products Co. (1964-84), Zapata Haynie, Inc. (1967-85).
SP = Sabine Pass, TX: Texas Menhaden Co. (1964-71).

Table 2

Estimated landings of gulf menhaden 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, 1964-85.

Fishing year	Landings in numbers-at-age (10^9)						Total landings (10^3 mt)	Nominal fishing effort (1000 vtw)
	0	1	2	3	4+	Total		
1964	a	3.33	1.50	0.12	a	4.95	409.4	272.9
1965	0.04	5.03	1.08	0.08	a	6.23	463.1	335.6
1966	0.03	3.31	0.87	0.03	a	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	a	4.58	373.5	382.3
1969	0.02	6.07	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	a	7.92	728.2	472.9
1972	0.02	3.05	1.73	0.09	a	4.89	501.7	447.5
1973	0.05	3.03	1.11	0.10	a	4.29	486.1	426.2
1974	a	3.85	1.47	0.06	0.0	5.38	587.4[b]	485.5
1975	0.11	2.44	1.50	0.46	a	4.51	542.6	538.0[c]
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	a	6.11	447.1	532.7
1978	0.0	6.79	2.74	0.05	a	9.59	820.0	574.3
1979	0.0	4.70	2.88	0.34	a	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

[a]$<0.005\times10^9$.
[b]Typographic error found in original NMFS data set and corrected in 1984.
[c]Correction made in tonnage for one vessel since analysis of Nelson and Ahrenholz (1986).

1982 fishing years (1977, 1980, and 1981 year classes) (Fig. 4). Since recruits to age-1 are a major portion of the population, the general trend in increasing recruitment to age-1 since 1964 is also reflected in increasing population size (age-1 and older fish).

Age-specific estimates of instantaneous fishing mortality rates (F) indicate that age-1 fish are not completely recruited to the fishery (F values for age-1 fish are considerably less than F values for age-2 and age-3 fish), while age-2 fish generally are fully recruited (Table 5). However, age-2 fish in 1974 (1972 year class) do not appear to be fully recruited (compare F_2 in 1974 with F_3 in 1975), nor do age-2 fish in 1981 (1979 year class; compare F_2 in 1981 with F_3 in 1982). The general conclusion drawn here compares closely with that of Ahrenholz (1981) based on tagged fish. Since the estimated F values were forced to converge towards a preset F_2, the estimates of F_3 and F_4 are, in effect, obtained from forward computations, so that an estimate of F_4 tends to diverge from its "true" value. This tendency is especially evident in the variability present in estimates of F_4. However, errors in population estimates of age-4 fish will have little effect on the following analyses because of their small contribution to the total adult population (Table 4). Furthermore, Ulltang (1977) noted that when F is high, convergence is rapid. Hence, even though a year class is well represented in the fishery for only three years, this time span appears adequate.

Short-term impacts of the fishery on the stock can be assessed by considering the exploitation rate (u) which is the fraction of the remaining stock removed by the fishery during some preset period of time (usually 1 year). Average exploitation rates (1964-83) were approximately 27% for age-1 fish and about 55% for age-2 and age-3 fish (Fig. 5). Annual natural mortality losses averaged about 54% for age-1 fish and 38% for age-2 and age-3 fish, although, in the absence of fishing, annual natural mortality losses would be about 67% for all ages. A general decline over time is noted both in the age-specific and population exploitation rates with fishing year. Population exploitation rate has declined from an average of 44% in the 1960's to 25% in the 1980's (Fig. 5). This decline, in part, represents the large increase in recruits to age-1 and population size compared with relatively smaller increases in landings.

Size-at-Age and Growth Analyses

Estimates of growth in length and weight are needed for estimating fishing yield, both from yield-per-recruit and population simulation analyses. Growth in length also is used to assess a density-dependent growth hypothesis and to reconstruct the spawners in terms of equivalent egg production for use in obtaining spawner-recruit relationships. Fork length (L_t, in mm) is estimated from age (t, in yr) on the basis of the von Bertalanffy (1938) growth function,

$$L_t = L_{inf}(1 - exp(-K(t - t_0))), \qquad (2)$$

Table 3
Estimated convergent F, age of convergent F, and ages used in virtual population analysis (VPA) for gulf menhaden by year classes, 1960-82.

Year class	Convergent F[a]	Age of convergence	VPA ages
1960	2.899[b]	4	4
1961	1.693[c]	3	3-4
1962	1.825	2	2-4
1963	2.362	2	1-3
1964	3.098	2	0-4
1965	1.099	2	0-3
1966	2.354	2	0-3
1967	2.474	2	0-4
1968	1.429	2	0-4
1969	1.995	2	0-4
1970	1.757	2	0-3
1971	1.830	2	0-4
1972	3.562[d]	3	0-3
1973	0.895	2	0-4
1974	1.422	2	0-4
1975	2.130	2	0-4
1976	0.996	2	1-4
1977	0.787	2	1-4
1978	1.193	2	1-4
1979	1.953	3	1-4
1980	1.055	2	0-4
1981	1.062	2	1-4
1982	1.220	2	1-3

[a]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).

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

[c]Convergent F for 1961 year class was obtained from the mean F for age-3 fish for year classes, 1964-79.

[d]Convergent F calculated from the mean F for 1971 and 1973 year classes.

where L_{inf}, K, and t_0 are parameters to be estimated. The computer program BGC3 (Abramson 1971) was used to obtain parameter estimates for Eq. (2). This program employs a nonlinear regression algorithm (Vaughan and Kanciruk 1982). Weight (W_t, in g) is then estimated from the weight-length relationship expressed in the linear form of the power function,

$$ln\ W_t = a + b\ ln\ L_t, \qquad (3)$$

where a and b are estimated parameters. Annual weight-length regressions based on Eq. (3) were calculated coastwide for each fishing year, 1964-85 (Table 6). The statistic, r^2, ranged from 0.92 to 0.98 for the annual coastwide weight-length regressions. Weighted averages of the estimated parameters were calculated by pooling fishing years 1964-85 and 1978-85 (Table 6). Weighting factors were catch in numbers by year (Table 2).

Mean fork length-at-age was calculated by quarter and aligned by year class so that the resultant growth curves represent the growth of a year class (or cohort) through its life span, rather than across several year classes during a single fishing year. Von Bertalanffy growth equation parameters were estimated for each year

Table 4
Estimated number of spawners (by age on 1 January and total) that produced the year class, estimated egg production from the spawning stock, and estimated numbers of recruits at age-0.5 and -1 for gulf menhaden by year classes, 1964-84.

	Spawners					Recruits (10^6)	
	Numbers-at-age (10^6)						
Year class	2	3	4	Total	Eggs (10^{12})	Age-0.5	Age-1
1964	2,992.7	240.5	7.5	3,240.7	38.6	23,159.4	13,357.7
1965	1,950.7	160.5	14.7	2,125.9	24.4	14,372.3	8,261.8
1966	1,525.0	61.2	8.1	1,594.3	16.1	22,909.7	13,199.6
1967	877.0	25.1	1.2	903.3	10.3	24,081.1	13,876.7
1968	1,921.0	97.3	1.2	2,019.5	22.4	46,799.3	26,943.2
1969	2,493.3	61.1	8.5	2,562.9	31.6	30,294.4	17,462.4
1970	5,292.2	82.2	3.5	5,377.9	55.6	36,925.8	21,271.8
1971	3,801.5	422.1	6.8	4,230.4	54.4	21,713.2	12,512.1
1972	3,670.5	172.1	39.6	3,882.2	45.5	35,879.7	20,688.2
1973	2,384.1	210.9	6.0	2,601.0	32.9	36,819.9	21,210.9
1974	5,009.1	127.5	7.5	5,144.1	74.2	24,192.2	13,955.6
1975	4,765.0	821.3	6.8	5,593.1	88.1	28,400.5	16,305.9
1976	3,132.2	661.3	7.8	3,801.3	58.9	54,129.7	31,230.1
1977	2,634.6	251.5	98.7	2,984.8	39.4	69,001.8	39,810.6
1978	7,592.8	129.2	20.4	7,742.4	80.6	58,612.0	33,816.2
1979	9,195.2	933.6	14.3	10,143.1	125.2	40,114.8	23,144.2
1980	8,287.1	1,389.6	110.4	9,787.1	125.2	65,029.0	37,461.3
1981	5,442.9	847.7	208.0	6,498.6	69.2	72,429.8	41,788.4
1982	8,997.3	971.1	95.4	10,063.8	103.8	53,745.6	31,008.5
1983	10,786.1	1,043.0	45.9	1,1875.0	143.3	NE	NE
1984	7,345.9	1,241.2	118.8	8,705.9	107.8	NE	NE

Table 5
Annual instantaneous fishing mortality rates (F) for gulf menhaden (ages 0 through 4) by fishing year, 1964-83. Minimum, maximum, and means for two time periods (1978-85 and 1964-85) are also given.

	Age				
Fishing year	0	1	2	3	4
1964	0.0006	0.6878	1.8254	1.6935	2.8992
1965	0.0037	1.0701	2.3621	1.8849	0.0952
1966	0.0014	1.1430	3.0052	2.8546	0.0648
1967	0.0013	0.8274	1.0991	1.9576	0.0000
1968	0.0022	0.6166	2.3476	1.3387	10.0000[a]
1969	0.0010	0.5275	2.3121	1.7729	0.0000
1970	0.0016	0.4247	1.4287	1.3934	0.0000
1971	0.0013	0.6571	1.9950	1.2670	10.5193[a]
1972	0.0007	0.5579	1.7569	2.2504	0.1975
1973	0.0016	0.3184	1.8286	2.2378	0.6084
1974	0.0002	0.3932	0.7081	1.8272	0.0000
1975	0.0049	0.3941	0.8747	3.5622	0.0429
1976	0.0000	0.7228	1.4220	0.8018	0.0000
1977	0.0000	0.3141	1.9149	1.4107	0.1087
1978	0.0000	0.3655	0.9959	1.1032	0.6698
1979	0.0000	0.3063	0.7896	1.0347	10.7091[a]
1980	0.0016	0.3475	1.1799	0.7994	1.7061
1981	0.0000	0.3264	0.6236	1.0844	0.3047
1982	0.0000	0.4920	1.0549	1.9530	14.0930[a]
1983	0.0000	0.3401	1.0622	1.0726	4.2333
Minimum	0.0000	0.3063	0.6236	0.7994	0.0000
Maximum	0.0049	1.1430	3.0052	3.5622	14.0930
Means:					
1978-85	0.0003	0.3630	0.9510	1.1745	5.2860
1964-85	0.0011	0.5416	1.5293	1.6650	2.8126

[a]Terminal F set equal to 10.0.

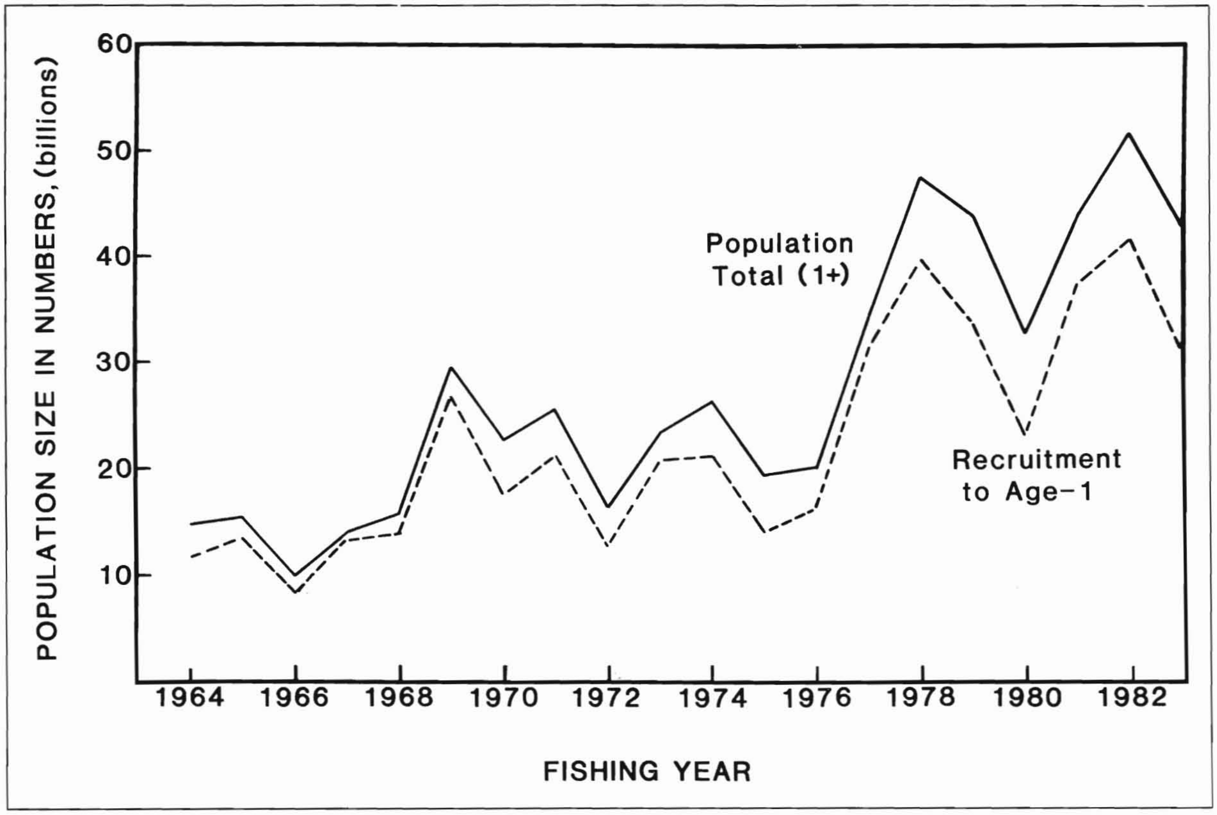

Figure 4
Population total (age-1 and older gulf menhaden) and recruits to age-1 on 1 January for each fishing year, 1964-83.

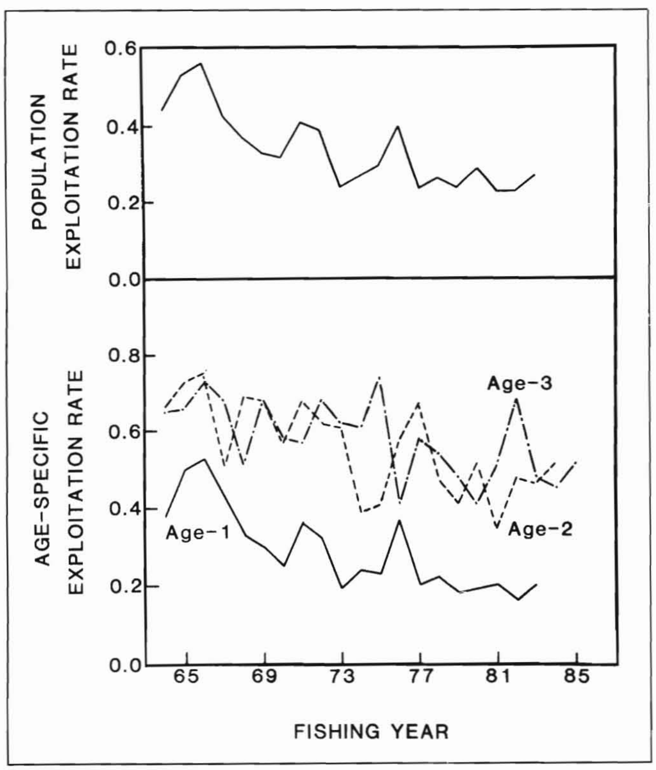

Figure 5
Annual estimates for gulf menhaden of (upper) population exploitation rates and (lower) age-specific exploitation rates (ages 1 through 3).

Table 6
Weight-length regression parameters for gulf menhaden by fishing year, 1964-85 (ln W = ln a + b ln L).

Fishing year	ln a	b	r^2
1964	−12.601	3.346	0.94
1965	−12.468	3.326	0.97
1966	−11.459	3.131	0.95
1967	−11.263	3.083	0.94
1968	−11.622	3.158	0.95
1969	−11.365	3.106	0.95
1970	−11.921	3.216	0.95
1971	−12.192	3.269	0.95
1972	−11.726	3.174	0.94
1973	−11.663	3.181	0.94
1974	−10.785	2.994	0.92
1975	−11.562	3.144	0.96
1976	−10.795	2.989	0.95
1977	−11.382	3.098	0.97
1978	−12.052	3.239	0.96
1979	−12.238	3.268	0.97
1980	−13.045	3.427	0.92
1981	−11.682	3.166	0.96
1982	−12.657	3.358	0.95
1983	−12.256	3.280	0.96
1984	−11.906	3.125	0.98
1985	−11.531	3.131	0.97
Weighted means			
1978-85	−12.131	3.253	—
1964-85	−11.878	3.205	—

Table 7

Estimated von Bertalanffy growth parameters for gulf menhaden obtained from mean quarterly lengths for year classes, 1960-82. For use in yield-per-recruit analyses, *not* for general use.

Year class	n	L_{inf}	K	t_0
1960	2	220.5	0.413	−4.307
1961	4	23,986.4	0.001	−4.759
1962	7	7,628.5	0.003	−5.470
1963	8	279.2	0.260	−1.514
1964	10	419.3	0.116	−2.254
1965	11	423.1	0.135	−1.729
1966	10	469.1	0.102	−2.027
1967	11	241.2	0.504	−0.486
1968	12	293.4	0.208	−1.957
1969	11	351.4	0.164	−2.102
1970	10	298.8	0.264	−1.170
1971	10	62,949.2	0.001	−3.124
1972	10	249.8	0.512	−0.497
1973	12	279.4	0.339	−1.026
1974	13	237.3	0.573	−0.394
1975	17	244.1	0.384	−1.135
1976	13	242.1	0.437	−0.613
1977	12	240.7	0.423	−0.925
1978	12	248.5	0.333	−1.457
1979	14	329.3	0.157	−2.203
1980	14	240.2	0.457	−0.425
1981	12	227.9	0.577	−0.373
1982	9	254.3	0.354	−1.054

class from 1964 through 1982 (Table 7). Lengths and corresponding weights for ages 0.50 to 5.00 (in increments of 0.25) were calculated for Eqs. (2) and (3) for used in the yield-per-recruit and population simulation models. Weighted averages across fishing years of the mean lengths-at-age were calculated for 1964-85 (Fig. 6, upper) and 1978-85 (Fig. 6, lower) mean conditions. Length-at-age for the 1964-85 mean conditions uniformly exceeds that for the 1978-85 mean conditions. However, the difference between the two growth curves decreases from 11.4 mm at age 1 to 0.5 mm at age 4.

The sizes of age-0.50 and age-0.75 gulf menhaden were found by Nelson and Ahrenholz (1986) to be biased upwards. Therefore, lengths at these ages were deleted when fitting the von Bertalanffy growth equation to mean coastwide lengths-at-age for use in estimating egg production from spawners (Table 8). No difference is noted between Tables 7 and 8 for year classes when no age-0 fish were landed (1960-63, 1976-79 and 1981-85). Large values of L_{inf} and correspondingly low values of K occur when curvature in the data is not pronounced, leading to estimation problems (Vaughan and Kanciruk 1982). However, interpolation of lengths and corresponding weights within the range of ages used in estimating the parameters are valid for use in yield-per-recruit (Table 7) and spawner-recruit (Table 8) analyses.

Estimates of annual mean weight-at-age for gulf menhaden in purse-seine catches were calculated to determine any trends in yield-per-recruit that could be expected in the fishery (Fig. 7). No specific trends in mean weight are noted, other than an apparent peak between 1973 and 1975 for age-1 through -3 fish.

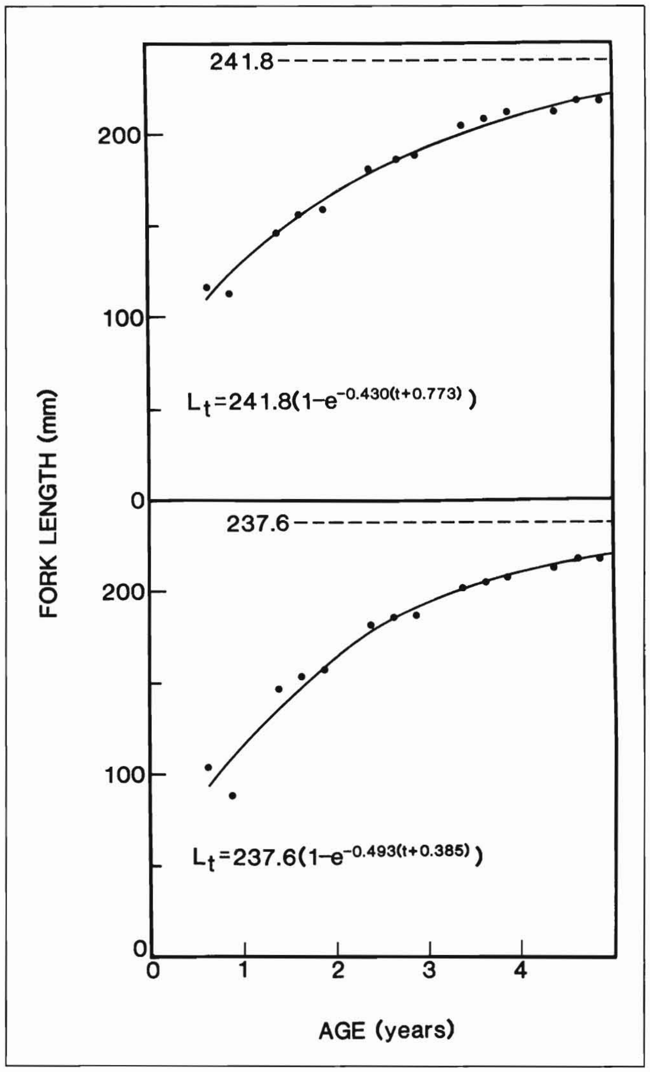

Figure 6

Von Bertalanffy growth curves estimated from mean length at age data for gulf menhaden based on (upper) 1964-85 fishing years, and (lower) 1978-85 fishing years.

Two aspects of density dependence are considered in this report. The first is concerned with the hypothesis that when stock size is large, the resultant competition among young-of-the year (age-0) fish will result in slower growth than when stock size is small. It is believed that if this mechanism occurs, it will express itself in the mean length-at-age for the second quarter (April - June) when fishing begins, especially for age-1 gulf menhaden. Reish et al. (1985) demonstrated density dependence in Atlantic menhaden for the mean length of age-1 fish, but not for older fish. Our results for gulf menhaden were not significant when mean length-at-age (ages 1-3) were regressed against recruits to age-1. The latter aspect of density dependence refers to the relationship between spawning stock size and subsequent recruitment and is discussed in the section "Spawner-Recruit Relationships."

Table 8
Estimated von Bertalanffy growth parameters for gulf menhaden obtained from quarterly mean lengths for year classes, 1960-82. Estimates obtained when mean lengths from age-0 deleted from analysis, for use in estimating egg production from spawners.

Year class	n	L_{inf}	K	t_0
1960	2	220.5	0.413	−4.307
1961	4	23,986.4	0.001	−4.759
1962	7	7,628.5	0.003	−5.470
1963	8	279.2	0.260	−1.514
1964	8	317.0	0.216	−1.333
1965	9	26,741.1	0.001	−3.558
1966	9	15,778.1	0.002	−3.319
1967	10	252.4	0.397	−0.881
1968	10	238.3	0.457	−0.568
1969	10	27,504.7	0.001	−5.051
1970	9	2,578.6	0.012	−3.667
1971	9	48,839.3	0.001	−3.417
1972	9	275.0	0.341	−1.104
1973	10	296.6	0.270	−1.437
1974	12	246.9	0.431	−0.933
1975	15	239.9	0.441	−0.800
1976	13	242.1	0.437	−0.613
1977	12	240.7	0.423	−0.925
1978	12	248.5	0.333	−1.457
1979	14	329.3	0.157	−2.203
1980	12	238.5	0.462	−0.469
1981	12	227.9	0.577	−0.373
1982	9	254.3	0.354	−1.054

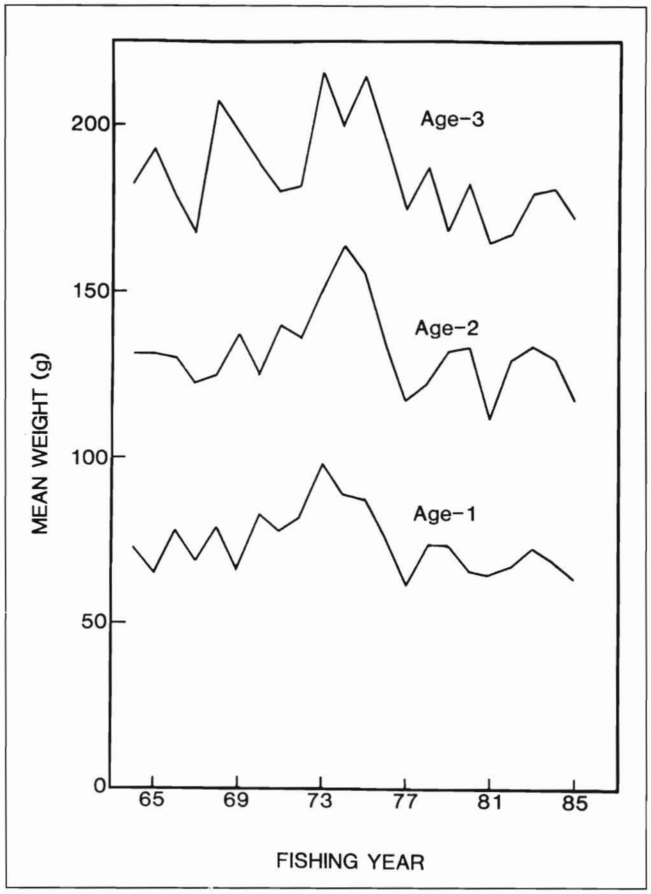

Figure 7
Mean annual weight of purse-seine landed gulf menhaden, ages 1, 2, and 3, for fishing years 1964-85.

Yield-per-Recruit Analyses

The computer program employed in this analysis (MAREA, Epperly et al. 1986) was modified from a multiple-gear extension (MGEAR, Lenarz et al. 1974) of the Ricker-type yield-per-recruit model to accommodate a multiple-area fishery. As described in Nelson and Ahrenholz (1986), yield is summed by time intervals such that individual lengths, weights, and estimates of natrual and fishing mortality can be inserted for each quarter. Two MAREA runs were made in which the data (Table 9) were developed based on mean conditions for 1964-85 and 1978-85. The age-at-entry into the fishery was 0.5 years, the age when gulf menhaden first appear in the landings. Fishing occurs primarily during the second and third quarters (April-September) on age-1 and age-2 fish (Table 9). Various multiples of the average fishing mortality (F-multiples) at each age were used to simulate increased or decreased fishing mortality (see example for 1978-85 mean conditions, Fig. 8). It is clear from this example, as well as for the 1964-85 mean conditions, that increasing the age-at-entry into the fishery beyond 1.5 years of age generally decreases the yield-per-recruit. No gain is realized when increasing age-at-entry from 0.5 to 1.5 years for F-multiple = 1.0. This results from the very high natural mortality rate (M = 1.1/year) and the typical growth parameter (K = 0.493/year for this example). Yield-per-recruit can only be increased by increasing the F-multiple, but this is not recommended due to a concern for the long-term stability of the stock through possible recruitment overfishing. Figure 8 appears different from Nelson and Ahrenholz (1986) because age-at-entry is plotted in different increments over different ranges of values. The step-like appearance to the isopleth diagram in Nelson and Ahrenholz (1986) results from fishing primarily during two quarters and plotting in increments of 0.25 years for the age-at-entry.

Additional MAREA runs were made for each fishing year from 1964 through 1983 (Table 10). Yield-per-recruit estimates are presented for these individual fishing years, and for 1964-85 and for 1978-85 mean conditions, for two levels of age-at-entry (0.5 and 1.25 years), and three levels of the F-multiple (0.4, 1.0, and 1.6). Annual yield-per-recruit varies from 6.87 g from the 1982 fishing year to 19.26 g from the 1977 fishing year (Fig. 9, left). Yield-per-recruit based on 1964-85 mean conditions was 15.84 g, while for mean conditions during the most recent year-classes (1978-85) it was 12.17 g. An inverse relationship is shown between annual yield-per-recruit and population size at the start of the fishing year (Fig. 9, right). This relationship results from the lag in landings behind the rapid increase in recruitment during the late 1970's. It is not suggested that there is a density-dependent relationship for yield-per-recruit.

Table 9

Input area of quarterly length, weight, and instantaneous fishing mortality rate by age for 1978-85 and 1964-85 mean conditions.

	1978-85 mean conditions			1964-85 mean conditions		
Age (yr)	Fork length (mm)	Weight (g)	F	Fork length (mm)	Weight (g)	F
0.50	84.0	9.6	0.0000	101.9	18.9	0.0007
0.75	101.8	18.3	0.0002	116.1	28.8	0.0004
1.00	117.6	29.3	0.0000	128.9	40.3	0.0001
1.25	131.5	42.1	0.0771	140.4	53.0	0.1468
1.50	143.8	56.3	0.2020	150.8	66.5	0.3503
1.75	154.7	71.4	0.0444	160.1	80.6	0.0325
2.00	164.3	86.9	0.0000	168.4	94.8	0.0002
2.25	172.8	102.4	0.2722	175.9	109.0	0.3864
2.50	180.3	117.6	0.5639	182.6	122.9	1.0080
2.75	186.9	132.3	0.1149	188.6	136.4	0.1352
3.00	192.8	146.3	0.0000	194.0	149.3	0.0002
3.25	198.0	159.5	0.4122	198.9	161.7	0.4302
3.50	202.6	171.8	0.6500	203.3	173.3	1.0380
3.75	206.7	183.3	0.1124	207.2	184.3	0.1969
4.00	210.2	193.8	0.0000	210.7	194.5	0.0000
4.25	213.4	203.5	0.4733	213.9	204.1	0.2155
4.50	216.2	212.3	2.7370	216.7	212.9	1.4580
4.75	218.7	220.4	2.0760	219.3	221.0	1.1390
5.00	220.9	227.6	—	221.6	228.5	—

Table 10

Estimates of yield-per-recruit (g) for gulf menhaden for each fishing year from 1964 through 1983, and for two sets of mean conditions (1978-85 and 1964-85 fishing years).

Fishing year	Age-at-entry (yr) 0.5	1.25	F-multiple 0.4	1.0	1.6	Population size[a] (10^6)
1964	17.16	17.15	11.79	17.16	19.42	11,315.6
1965	18.01	17.99	13.22	18.01	19.65	11,761.0
1966	18.60	18.58	14.06	18.60	20.29	7,479.8
1967	17.01	17.01	11.15	17.01	19.33	10,707.6
1968	17 33	17.31	12.50	17.33	19.29	12,074.3
1969	10.41	10.39	5.83	10.41	13.37	22,411.9
1970	15.32	15.30	9.56	15.32	18.05	17,348.7
1971	17.52	17.50	12.43	17.52	19.50	19,359.2
1972	15.68	15.68	11.10	15.68	17.35	12,444.5
1973	15.12	15.10	10.18	15.12	17.55	17,686.7
1974	16.33	16.33	9.58	16.33	19.79	20,018.5
1975	16.53	16.47	10.93	16.53	19.20	14,848.7
1976	18.59	18.59	11.88	18.59	21.14	15,272.9
1977	19.26	19.26	13.20	19.26	21.39	25,988.6
1978	13.98	13.98	8.32	13.98	16.78	36,120.0
1979	13.36	13.36	8.32	13.36	16.22	33,390.1
1980	15.43	15.43	9.28	15.43	18.31	25,013.7
1981	10.21	10.21	5.83	10.21	12.43	33,390.7
1982	6.87	6.87	3.92	6.87	9.22	39,385.5
1983	13.57	13.57	8.49	13.57	16.09	32,573.0
			Mean conditions			
1978-85	12.17	12.17	7.88	12.17	14.20	33,312.2
1964-85	15.84	15.83	10.64	15.84	18.06	20,929.5

[a]Population size based on ages ≥1 on 4 April.

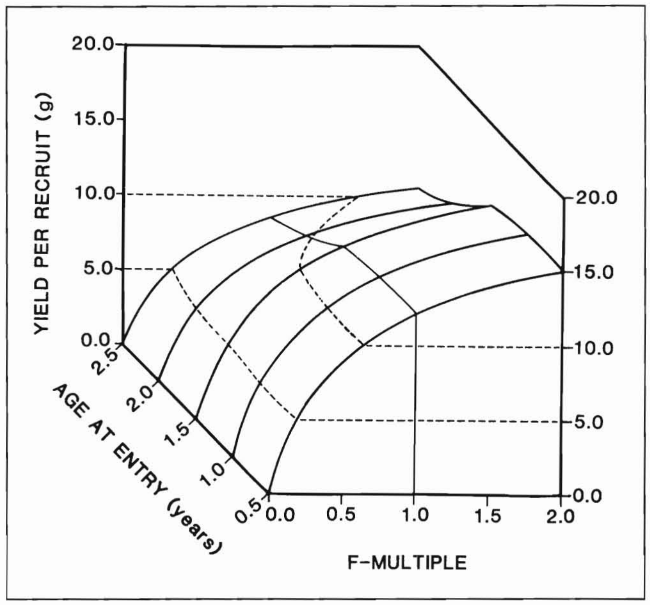

Figure 8

Overall yield-per-recruit isopleth for gulf menhaden under 1978-85 mean conditions of growth and multiples of fishing mortality by 3-month interval (F-multiple = 1.0).

Surplus Production Models

Surplus production models are typically used to obtain estimates of maximum sustainable yield from yield and fishing effort data (Vaughan et al. 1984). When using these models, yield is assumed to be proportional to population abundance and fishing effort proportional to fishing mortality. Theoretically, plotting catch against effort should give a dome-shaped curve, which is not the case for gulf menhaden data, although the points might lie along the ascending limb of such a curve (Fig. 10). When relating fishing effort (E) to the instantaneous fishing mortality rate (F), the catchability coefficient (q) is assumed to be constant; i.e.,

$$F = q E, \tag{4}$$

where the unit of fishing effort, E, is defined as vessel-ton-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 a reliable measure of fishing mortality 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 non-schooling species [see discussion of "dynamic aggregation process" in Clark and Mangel (1979)]. The concern here is that severe stock depletion could occur before it was indicated by an analysis of yield and CPUE data.

To demonstrate that the population catchability coefficient, q, for gulf menhaden is not constant but dependent upon the population size, it was estimated by solving Eq. (4) for q ($=F/E$) for each fishing year from 1964 through 1983 (Fig. 11) and compared with the population size for the same fishing year (Fig. 12). To calculate the population (all ages combined) instantaneous fishing mortality rate (F), it was first necessary to compute the population exploita-

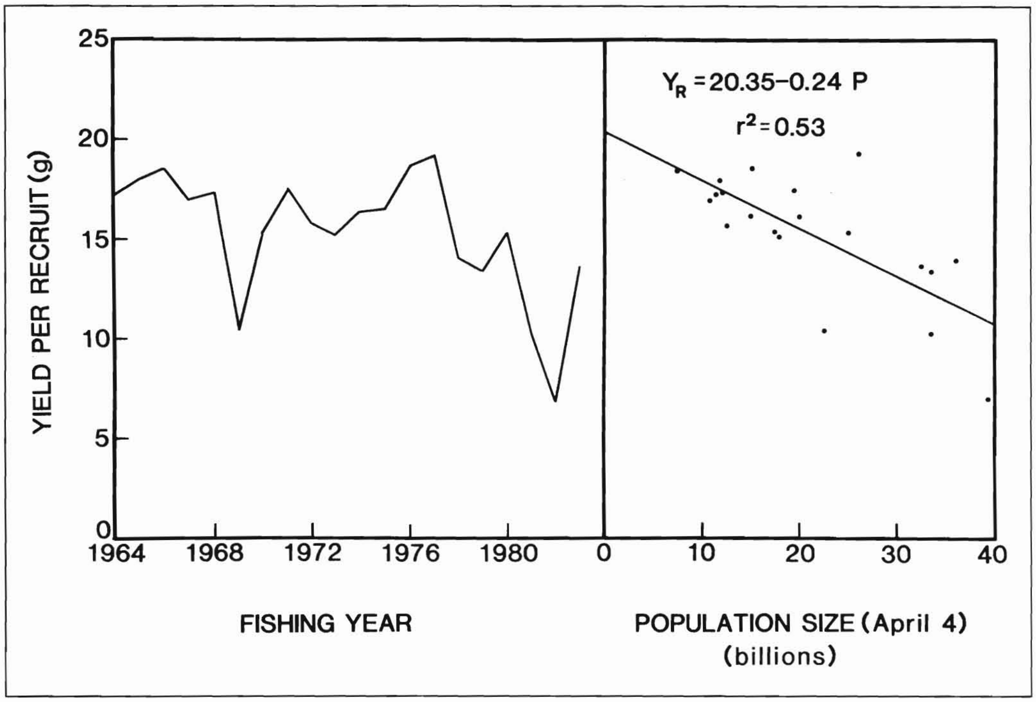

Figure 9

Annual estimates of yield per recruit for gulf menhaden plotted against (left) fishing year, and (right) population size (age-1 and older fish).

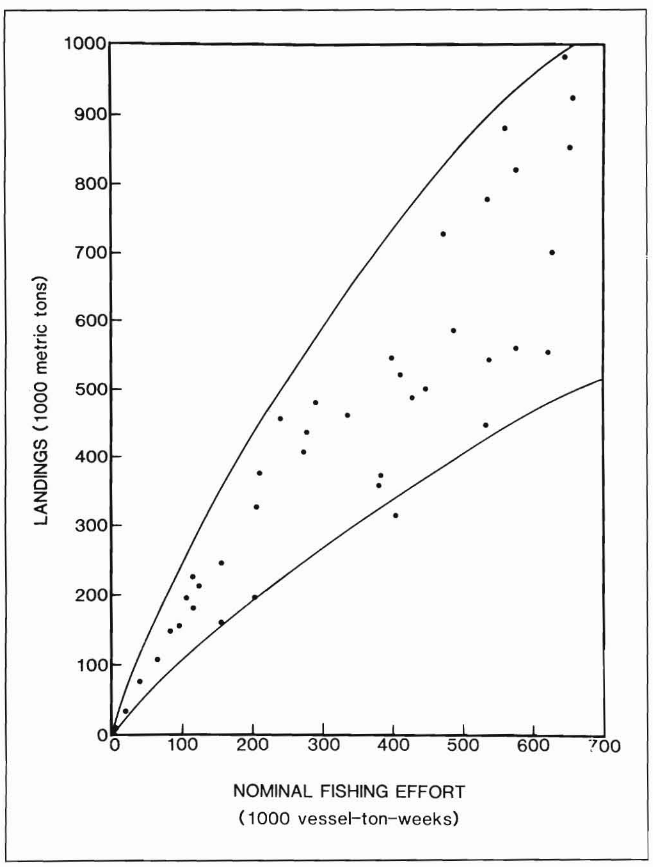

Figure 10

Gulf menhaden landings plotted against nominal fishing effort for the 1946-85 fishing years. Solid curves represent range in landings depending on fishing effort.

tion rate (u) by comparing numbers caught in a fishing year (for all ages 1-4) with the population size (for all ages 1-4) on 4 April for that year (Table 11). The population F is then calculated iteratively from the equation:

$$F = u\ (F + M)/(1 - exp(-\ (F + M))), \tag{5}$$

where u and M (=1.1/year) are known. Estimates of q range between 6.9×10^{-7}/year·vessel-ton-week in 1982 when the population size was 39.4 billion (age-1 and older fish) and 43.5×10^{-7}/year·vessel-ton-week in 1965 and 1966 when the population sizes were 11.8 and 7.5 billion, respectively (Table 11). As noted in Nelson and Ahrenholz (1986), there is a pronounced inverse relationship between the catchability coefficient and population size (Fig. 13). Furthermore, the historical trend that they noted continues to be evident with the addition of seven more years of data; i.e., there appears to be a functional curve. With generally increasing population size since 1964, the catchability coefficient has declined to a level in 1982 that is one-sixth that of 1965-66.

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

$$E' = E\ q/q_a, \tag{6}$$

where E' is a unit of "effective" fishing effort (Fig. 13). Note that while nominal effort has increased rapidly, effective fishing effort has declined since 1966.

The computer program PRODFIT (Fox 1975), which accounts for non-equilibrium conditions, is used to estimate parameters for different surplus production models depending on the value of m in the following equation:

$$U = (A + B\ E')^{1/(m-1)}, \tag{7}$$

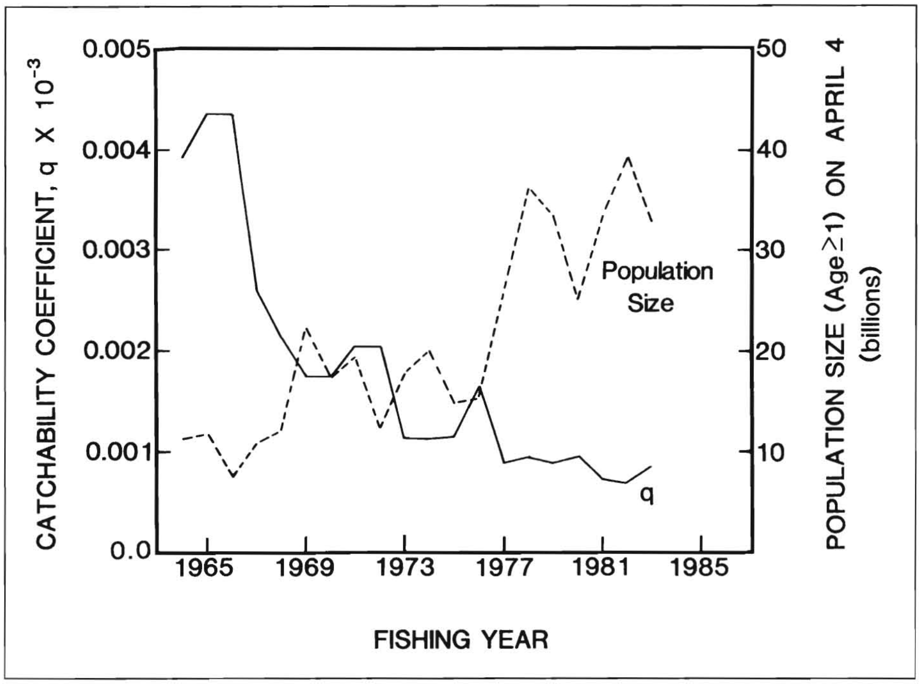

Figure 11

Catchability coefficient (q) and population size (age-1 and older) for gulf menhaden plotted against fishing year, 1964-83.

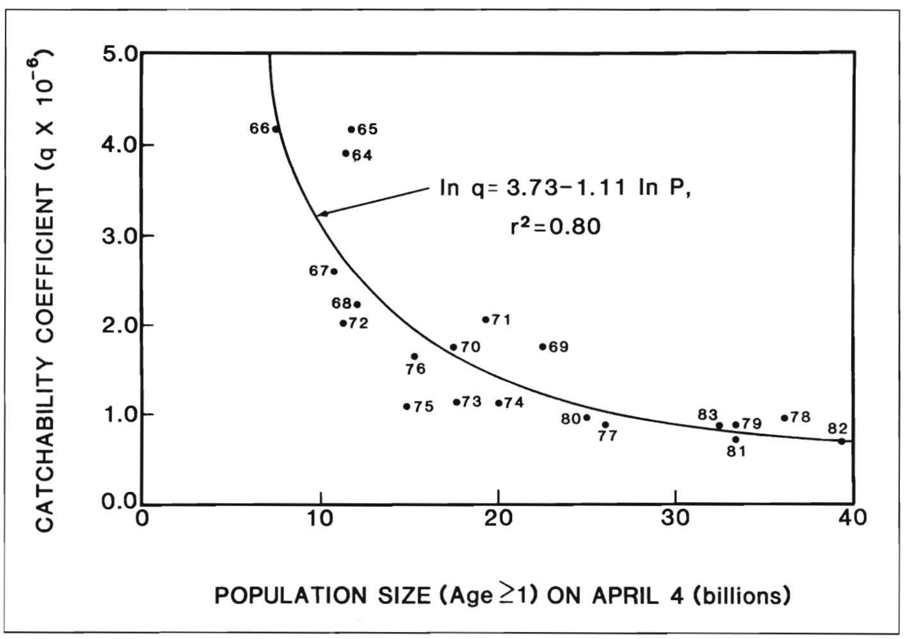

Figure 12

Catchability coefficient (q) plotted against population size (age-1 and older) of gulf menhaden. Also shown is linearized regression of ln q against ln P (solid curve).

Table 11

Estimated population size (ages 1-4) on 4 April, numbers landed (ages 1-4), population exploitation rate (*u*), population instantaneous fishing mortality rate (*F*, yr^{-1}), catchability coefficient (*q*, yr^{-1} vessel-ton-weeks^{-1}), and effective fishing effort (*E'*, vessel-ton-weeks) for gulf menhaden by fishing year, 1964-85.

Fishing year	Population size (10^9)	Numbers landed (10^9)	Population *u*	*F*	$q(10^{-6})$	E' (10^3)
1964	11.32	4.95	0.437	1.071	3.92	272.9
1965	11.76	6.19	0.526	1.459	4.35	371.8
1966	7.48	4.21	0.563	1.658	4.35	422.5
1967	10.71	4.62	0.431	1.048	2.59	267.1
1968	12.07	4.51	0.374	0.850	2.22	216.7
1969	22.41	7.39	0.330	0.716	1.74	182.4
1970	17.35	5.60	0.323	0.695	1.74	177.2
1971	19.36	7.90	0.408	0.965	2.04	245.9
1972	12.44	4.87	0.392	0.910	2.03	231.9
1973	17.69	4.24	0.240	0.477	1.12	121.6
1974	20.02	5.38	0.269	0.549	1.13	140.0
1975	14.85	4.40	0.296	0.620	1.15	158.1
1976	15.27	6.17	0.404	0.951	1.65	242.4
1977	25.99	6.11	0.235	0.465	0.87	118.5
1978	36.12	9.59	0.265	0.539	0.84	137.4
1979	33.39	7.92	0.237	0.470	0.88	119.7
1980	25.01	7.15	0.286	0.593	0.95	151.2
1981	33.39	7.54	0.226	0.444	0.71	113.1
1982	39.39	9.01	0.229	0.451	0.69	114.9
1983	32.57	9.80	0.273	0.559	0.85	142.6
1984	—	11.12	—	—	—	—
1985	—	11.15	—	—	—	—

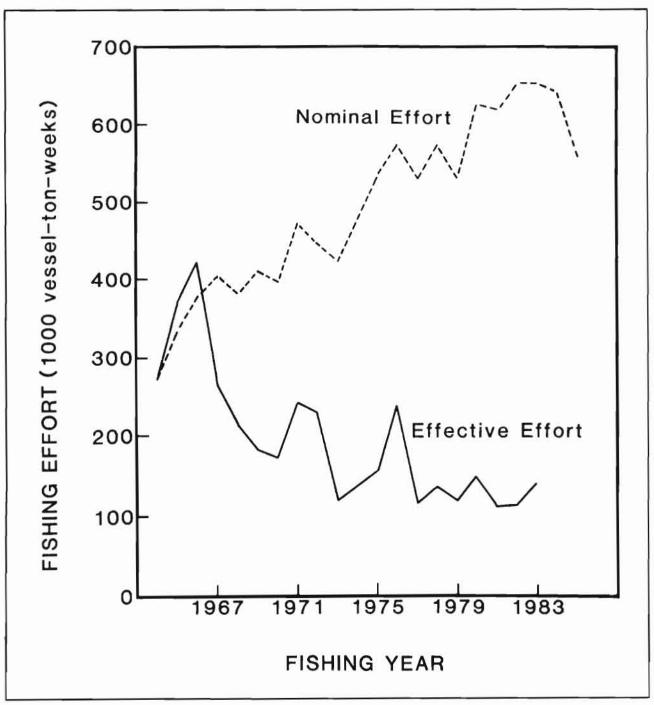

Figure 13

Nominal and effective fishing effort for gulf menhaden plotted against fishing year, 1964-1985.

where *U* is catch-per-unit-effort, and *A*, *B*, and *m* are parameters to be estimated. The generalized production model of Pella and Tomlinson (1969) is obtained when *m* is allowed to be estimated freely. However, when *m* is forced equal to 2.0, the Schaefer model (Schaefer 1954, 1957) is obtained, and when *m* is forced equal to 1.0, the Gompertz model (Fox 1970) is obtained. The program PRODFIT also allows the analyst to enter the number of significant age classes to be entered in the analysis (i.e., this is used in estimating parameters under non-equilibrium conditions). Those age classes contributing at least 10% to the landings in numbers served as the basis for determining the number of significant age classes for each fishing year in the analysis (1946-85). Estimates of MSY based on 1946-85 fishing years range from 621.1 KMT when *m* is estimated freely ($m = 0.99$; Pella-Tomlinson model) to 696.4 KMT when *m* is forced equal to 2.0 (Schaefer model) (Fig. 14). The scatter evident in Figure 14 illustrates why little confidence is placed in this approach to estimating MSY. More confidence is placed in population simulation models, which are discussed later.

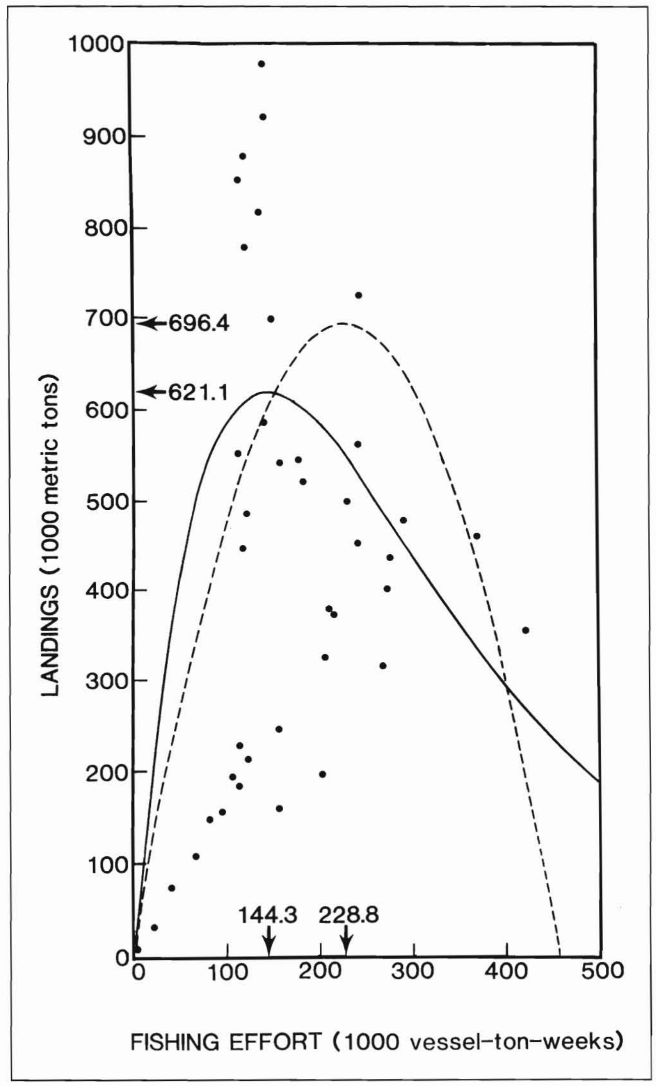

Figure 14

Catch of gulf menhaden plotted against effective fishing effort for 1946-85 fishing years. The solid curve is the Pella-Tomlinson generalized production model, and the dashed line is the parabolic (Schaefer) production model.

With MSY estimates ranging between 620 and 700 KMT, one would expect that recent levels of landings could not be maintained. However, these high levels of landings are occurring with relatively low fishing mortality (i.e., 25% mean exploitation rate in the 1980's compared with 44% mean exploitation rate in the 1960's; Table 11) and declining effective fishing effort. The decline in exploitation rate (and effective fishing effort) appears to be the result of increased population size due to recent high recruitment (Table 4). The next section provides some insight into whether there is sufficient spawning stock to guard against recruitment failure or whether there are sufficient numbers of recruits to sustain the stock.

Spawner-Recruit Relationships

An important question in population dynamics and in fisheries management concerns the degree of dependency between the number of spawners and the number of subsequent recruits to the stock. If there is no such dependency, 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 pre-recruit juveniles. If there is a quantifiable relationship between spawners and recruits, then management can be designed to maximize the landings or some other objective based on this relationship. Such a relationship was examined for gulf menhaden using the Ricker (1954) model. The Ricker model was selected over the Beverton and Holt (1957) model based on arguments by Nelson and Ahrenholz (1986) favoring a dome-shaped spawner-recruit relationship. The primary biological argument for the Ricker model is that adult filter-feeding menhaden are known to ingest their own eggs.

Estimation of the number of recruits to age-0.5 and to age-1 has been described in the VPA section (Table 4). Estimation of spawners follows the description given in Nelson and Ahrenholz (1986). The number of mature spawners for each year on 1 January is given by age (Table 4), where spawning peaks in December and January and all fish mature by the end of their second year (Lewis and Roithmayr 1981). The total number of spawners for each recruitment year (1 January) is given by the sum from age 2.00 through age 4.00 (Table 4).

Potential egg production has also been 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):

$$\ln(EGGS) = -9.8719 + 3.8775 \ln L, \qquad (8)$$

where $EGGS$ equals numbers of eggs produced per female, and L equals estimated fork length (mm). Mean length-at-age for the first quarter (Table 12) was calculated from the von Bertalanffy growth curves given in Table 8. The expected egg production per female of a given age was calculated using Eg. (8) and the lengths given in Table 12. Assuming a 50:50 sex ratio, multiplying one-half population numbers at age (Table 4) by the expected egg production per female-at-age gives the potential egg production per individual-at-age (Table 12). Summing across ages for the same fishing year gives the numbers of spawners as potential eggs (Table 4).

Spawners as numbers of adults on 1 January (Table 4) ranged between 903.3×10^6 in 1967 and $11{,}875.0 \times 10^6$ fish in 1983. Spawners as potential eggs on 1 January ranged between 10.3×10^9 eggs in 1967 and 143.3×10^9 eggs in 1983. Low to moderate spawning stock size was the rule from 1964 to 1977, and medium to high spawning stock size from 1978 to 1984. High recruitment in 1977, 1980, and 1981 year classes resulted in large spawning stocks in 1979, 1982, and 1983 (as age-2 fish). Since 1964, the proportion of age-2 spawners to the spawning stock has been fairly consistent, ranging between 82% and 98% in numbers and between 69% and 97% as eggs (Fig. 15). Since the mid-1970's, the contribution of age-2 spawners to the spawning stock has averaged about 88% in numbers and about 80% as eggs.

Table 12

Estimated mean fork length and potential egg production at age on 1 January (2-4 yr) for gulf menhaden by fishing year, 1964-84.

Fishing	Lengths (mm)			Age-specific egg production (10^{12})		
year	2	3	4	2	3	4
1964	169.9	188.3	213.4	34.30	4.11	0.21
1965	167.3	192.3	212.5	21.06	2.97	0.40
1966	162.6	192.9	214.7	14.74	1.15	0.23
1967	168.6	192.6	212.7	9.76	0.47	0.03
1968	166.4	198.8	216.7	20.31	2.05	0.04
1969	172.1	197.5	229.0	30.04	1.26	0.31
1970	164.7	198.4	228.6	53.77	1.72	0.13
1971	172.8	191.7	216.1	46.53	7.73	0.20
1972	168.8	197.2	208.8	41.02	3.52	1.01
1973	171.5	197.4	221.6	28.34	4.32	0.19
1974	179.5	203.1	225.7	71.05	2.92	0.26
1975	179.5	207.1	234.7	67.59	20.28	0.27
1976	177.2	207.2	226.7	42.26	16.36	0.27
1977	170.0	201.6	228.4	30.26	5.60	3.56
1978	164.9	194.9	217.4	77.51	2.52	0.61
1979	170.8	192.2	211.0	107.57	17.26	0.38
1980	170.0	194.9	209.9	95.20	27.12	2.87
1981	158.8	192.2	210.7	48.01	15.67	5.49
1982	162.3	183.6	208.2	86.35	15.03	2.41
1983	169.9	190.5	204.7	123.62	18.63	1.08
1984	167.9	195.3	208.2	80.42	24.42	2.99

Parameters of the Ricker model were estimated by nonlinear regression from the equation:

$$R = aS \exp(-bS), \qquad (9)$$

where R equals recruits (numbers at age 0.5 or age 1), S equals spawners (number of adults or potential eggs), and a and b are parameters to be estimated. Four regressions were calculated from the data presented in Table 4 (Table 13). In all cases parameter estimates for both a and b were significantly greater than zero, indicating a significant relationship.

As illustrated in Figure 16 for the Ricker curve based on spawners in numbers and recruits to age-1, considerable scatter (or unexplained variability) remains due to environmental conditions or measurement error. Given the scatter evident from these regressions, their use is of limited value; e.g., not useful for predicting future absolute population sizes. However, these relationships are statistically significant, so that the number of future recruits does depend to some appreciable extent upon the size of the spawning stock which produced them, and hence can be used in population simulation projections to investigate sustainable yield for a variety of F-multiples and to determine MSY.

Ricker models obtained in these analyses suggest that maximum equilibrium stock size (age-2 and older fish on 1 January) could be between 19 and 24 billion fish (Table 13). However, stock size for maximum recruitment (about 30 billion age-1 fish) would occur at

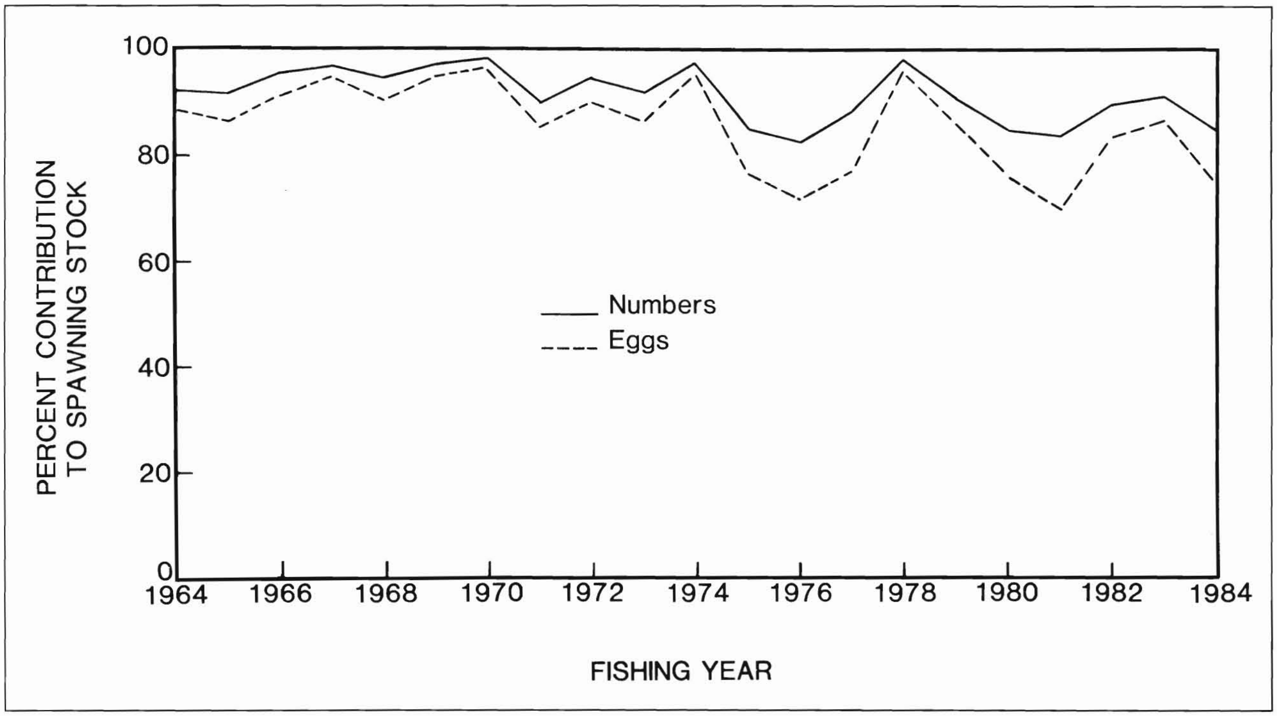

Figure 15

Contribution of age-2 spawners (%) to total spawning stock (Numbers) and to total egg production (Eggs) of gulf menhaden, 1964-84.

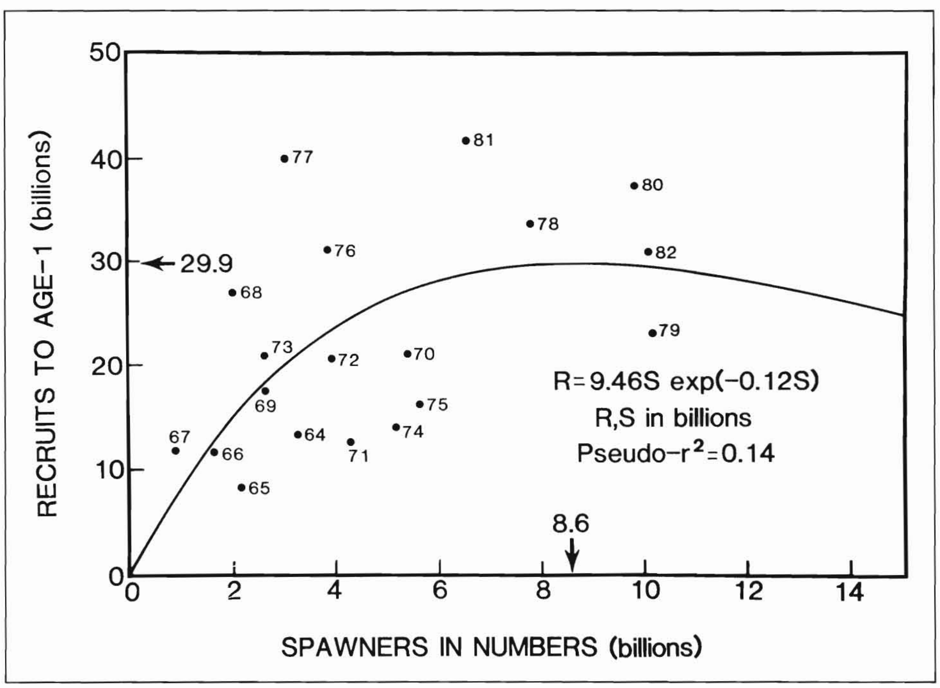

Figure 16

Numbers of gulf menhaden recruits (R) plotted against numbers of spawners (S) for year classes, 1964-82. Curve represents the fitted Ricker function.

Table 13

Estimates of Ricker spawner-recruit parameters, maximum equilibrium stock size (S_r), stock size for maximum recruitment (S_m) and maximum recruitment (R_m) for models regressing number of recruits (age-0.5 on 4 July or age-1 on 1 January) on numbers of spawners (ages 2-4) and on potential egg production from spawners for 1964-82 year classes of gulf menhaden.

Recruits	a(SE)	b(SE)	S_r	S_m	R_m
		Spawners as numbers (10^9)			
Age-0.5	16.42(3.65)	0.117(0.034)	24.02	8.58	51.86
Age-1.0	9.46(2.11)	0.116(0.034)	19.31	8.59	29.91
		Spawners as eggs (10^{12})			
Age-0.5	1.49(0.35)	0.011(0.003)	—	90,909.09	49.77
Age-1.0	0.86(0.20)	0.011(0.003)	—	90,909.09	28.69

about 9 billion spawners (Table 13). Since 1978, stock size has averaged 9.3 billion fish and recruits to age-1 have averaged 33.4 billion (Table 4). Although the spawner-recruit relationships are marginal, recent mean conditions appear to indicate that recruitment is at or near maximum. However, environmental conditions appear to be more important in regulating recruitment, so greater (or lesser) recruitment values may occur. It is not suggested that maximizing stock size (19-24 billion fish) is necessarily an attainable goal for management given the marginal nature of the spawner-recruit relationship. Some of the gains in landings already may be evident in the recent high landings that have come from high recruitment and population size since 1978.

Population Simulation Models

Estimating maximum sustainable yield, based on biological characteristics of the population, is more preferable than estimates based on yield and fishing effort (surplus production models discussed earlier in this report). Walters (1969) developed a simulation model (computer program POPSIM), which allows the inclusion of estimates of growth in weight, a spawner-recruit relationship, and natural and fishing mortality rates. Estimation of weight-at-age was discussed in the section "Size at Age And Growth Analyses." In addition to the two estimated Ricker spawner-recruit models described in the previous section (based on recruits to age-1), a third spawner-recruit relationship was developed on the basis of the uniform probability density function for the range in observed recruitment to age-1 on 1 January during the period 1964-82 (8.3 to 41.8 billion fish) (Table 4). Fishing mortality can be different for each age class, but must be constant between seasons for which F is greater than zero. Because of between-season limitation on fishing mortality rates in the Walters (1969) model, no fishing is assumed to occur before age-1, and fishing on age 1-4 fish is assumed to occur only during the second and third quarters (April-September). These limitations are not thought to have any significant effect on the model results, since few age-0 fish have been caught since the mid-1970's and the fishing season is restricted by law to the period from mid-April to mid-October. Natural mortality (M) is assumed equal to 1.1/year (67% per year) as in previous analyses.

Numerous POPSIM runs were made for three spawner-recruit relationships (spawners in numbers, spawners as eggs, and random recruitment) and for two sets of mean conditions (1964-85 and 1978-85). For each of these six conditions (3 × 2), population simulations or projections were run for a series of F-multiples ranging from 0.2 to 3.0. The projections were for at least 50 years (e.g., a 25-year projection is shown in Figure 17), and produced estimates of population-size-at-age, and yield to the fishery for each year. For most runs involving either of the Ricker spawner-recruit relationships, only a few years of the simulation were required for equilibrium (sustainable) conditions to be attained. Obviously, no such equilibrium conditions are attainable from the random recruitment model. Table 14 presents the equilibrium conditions obtained from F-multiples ranging from 0.2 to 2.0 for the Ricker model with spawners in numbers and using 1964-85 mean conditions. F-multiples greater than 2.0 would ultimately lead to a population crash. Estimates of MSY for the 1964-85 mean conditions range from 803 KMT (F-multiple of 1.0, spawners as eggs) to 825 KMT (F-multiple of 1.0, spawners in numbers), while estimates of MSY for the 1978-85 mean conditions range from 705 KMT (F-multiple of 1.5, spawners as eggs) to 713 KMT (F-multiple of 1.5, spawners in numbers) (Table 14).

Two features become evident after comparing the equilibrium yields between 1964-85 and 1978-85 mean conditions for the two Ricker models (spawners in numbers, Fig. 18). First, the 1964-85 mean conditions have a higher MSY than do the 1978-85 mean conditions; secondly, the 1978-85 mean conditions appear less susceptible to population collapse than do the 1964-85 mean conditions at higher values of the F-multiple. The higher MSY estimate, obtained for the 1964-85 mean conditions compared with the 1978-85 mean conditions, is probably due to the higher mean weight of individuals landed during the full 1964-85 period compared with the recent 1978-85 period (Fig. 7). The lower MSY estimate is obtained in spite of higher recruitment levels since 1978. The apparent decrease in susceptibility to population collapse is based on lower exploitation rates (Fig. 5), a shift to higher F for MSY (Fig. 18), and results from the higher recruitment levels since 1978. Fifty-year mean yield can be compared between two

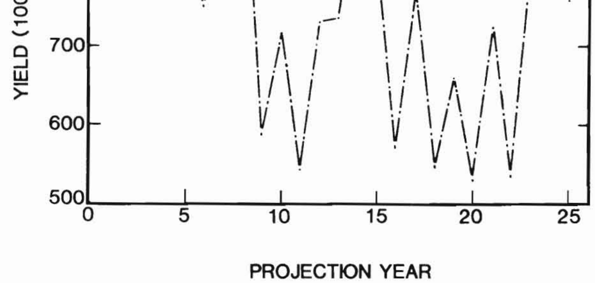

Figure 17

Population projections for 25 years with F-multiple = 1.0 under 1978-85 mean conditions for gulf menhaden. Three superimposed curves are for Ricker model with spawners in numbers (solid line), Ricker model with spawners as eggs (dashed line), and random recruitment model (dot-dashed line).

Table 14

Annual age-specific fishing mortality rates for gulf menhaden expressed as multiples of the average fishing mortality rate at age, actual fishing mortality rates at age used in the population simulation model, population size in biomass and numbers and sustainable yield based on Ricker spawner-recruit relationship between numbers of recruits at age-1 and spawners as numbers (ages 2-4) for 1964-85 mean conditions. Additional maximum sustainable yield (MSY) estimates obtained for 1978-85 mean conditions and for spawner-recruit curves based on spawners as eggs.

	Actual *F* at age					Population		Sustainable
F-multiple	0	1	2	3	4	Biomass (10^3 mt)	No. (10^9)	yield (10^3 mt)
0.0	0.0	0.000	0.000	0.000	0.000	2596.8	40.2	0.0
0.2	0.0	0.109	0.306	0.333	0.563	2394.1	40.1	366.0
0.4	0.0	0.217	0.613	0.667	1.126	2221.1	39.5	580.2
0.6	0.0	0.326	0.919	1.000	1.689	2056.8	38.3	710.6
0.8	0.0	0.435	1.225	1.333	2.252	1890.7	36.4	780.8
1.0	0.0	0.543	1.531	1.666	2.815	1709.2	33.9	803.3
1.2	0.0	0.652	1.838	2.000	3.378	1504.9	30.6	780.7
1.4	0.0	0.761	2.144	2.333	3.941	1271.7	26.4	713.5
1.6	0.0	0.869	2.450	2.666	4.504	997.3	21.1	597 3
1.8	0.0	0.978	2.756	3.000	5.067	677.2	14.5	428.2
2.0	0.0	1.807	3.063	3.333	5.630	295.8	6.4	196.2
MSY for Ricker spawner-recruit relations								
1978-85 mean conditions								
Spawners as numbers:								
1.5	0.0	0.547	1.427	1.760	7.927	1363.2	34.0	712.6
Spawners as eggs:								
1.5	0.0	0.547	1.427	1.760	7.927	1355.3	33.8	704.8
1964-85 mean conditions								
Spawners as numbers:								
1.0	0.0	0.543	1.531	1.666	2.815	1709.2	33.9	803.3
Spawners as eggs:								
1.1	0.0	0.598	1.648	1.833	3.097	1666.2	33.5	825.1

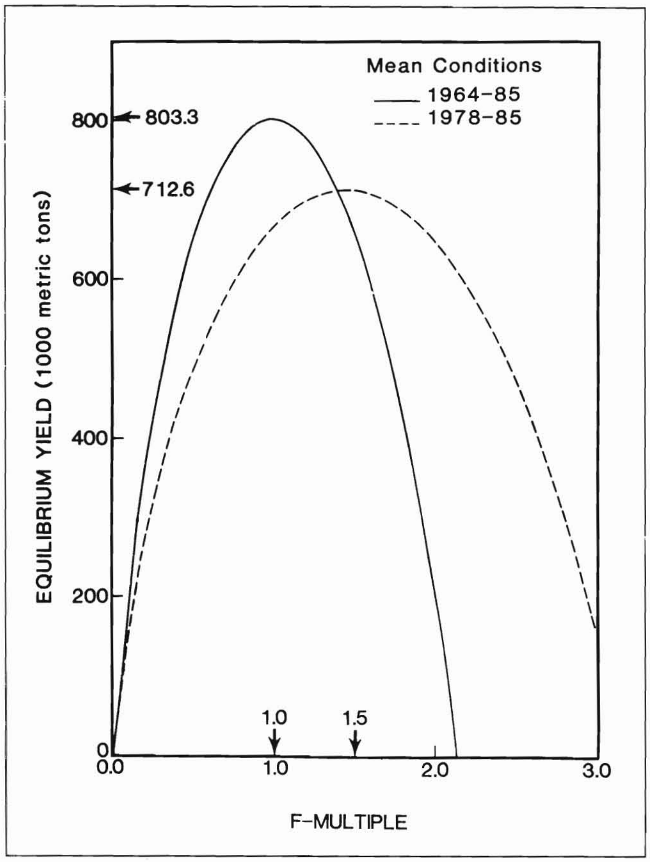

Figure 18

Equilibrium (or sustainable) yield curves from gulf menhaden population simulation model using Ricker spawner-recruit relation with spawners in numbers. Two superimposed curves are for 1964-85 mean conditions (solid line) and for 1978-85 mean conditions (dashed line).

of the spawner-recruit relationships (Ricker model with spawners in numbers and random recruitment) for the 1978-85 mean conditions (Fig. 19). If recruitment is random and independent of stock size, a population crash is unlikely. However, the curve for the random recruitment model appears to be approaching an asymptotic value for 50 year mean yield as the *F*-multiple increases. The yearly average for the asymptotic MSY from the random recruitment model is about 750-800 KMT for 1978-85 mean conditions (Fig. 19).

The MSY estimates from the population simulation approach (705-825 KMT) are generally higher than those obtained from the surplus production models (620-700 KMT). I expect that estimates of MSY from the population simulation model would be more realistic than those obtained from the surplus production models which are based solely on catch and effort data.

Management Implications

The gulf menhaden fishery is conducted within the territorial sea and offshore of five coastal states (Florida to Texas). All states voted in favor of a cooperative management plan under the Gulf States Marine Fisheries Commission (GSMFC) in 1977 (Christmas and Etzold 1977). This plan was revised and adopted in 1983 (Christmas et al. 1983). Since management authority is vested in the individual states, some regulations are area-specific on a state or county basis, but other regulations, such as length of fishing season (mid-April through mid-October), are common to all states. No state controls or limits the catch or fishing effort of vessels.

Both landings and fishing effort have increased dramatically since 1946 (Fig. 2), with high record landings during the 1984 fishing season (982.8 KMT) and record high nominal fishing effort during the 1983 fishing season (655,800 vessel-ton-weeks). Although an earlier stock assessment revealed that levels of stock biomass were sufficient to produce historical landings (Nelson and Ahrenholz 1986), a new analysis was deemed necessary to determine if more recent high harvests are due to (a) an increase in effective fishing effort and availability of the stock, or (b) an increase in stock size due to exceptionally large year classes in recent years. Given either of the above conditions, it is unlikely that the fishery can sustain these high levels of harvest indefinitely;

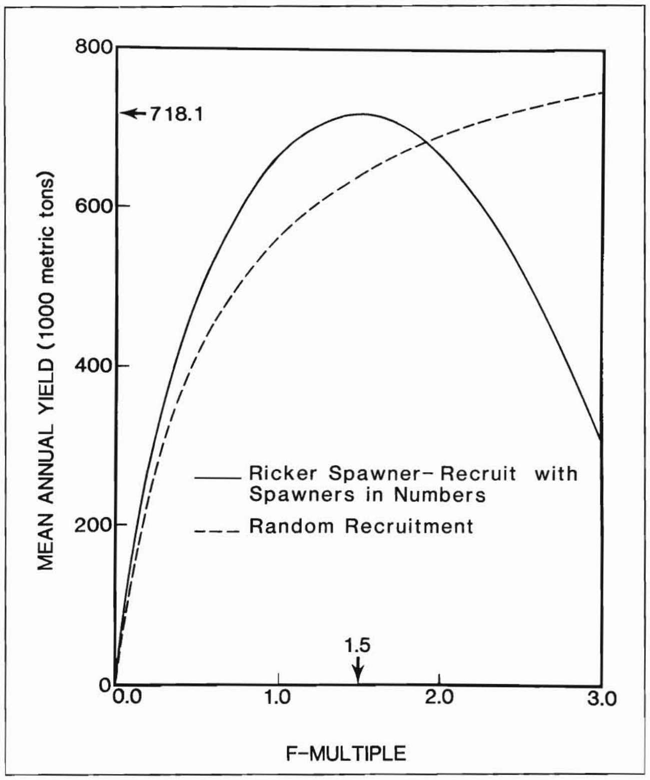

Figure 19

Fifty year mean yield for 1978-85 mean conditions from gulf menhaden population simulation model. Two superimposed curves are for Ricker model with spawners in numbers (solid line) and random recruitment model (dashed line).

landings eventually will be reduced. If condition (a) is prevalent, stock damage may occur and harvests would drop below levels that would occur if condition (b) is prevalent where no stock damage is expected to occur.

Recruitment to age-1 (on 1 January) has varied between 8.3 and 41.8 billion fish (Table 4), with many of the greater values occurring since 1977. Greater values for population size and spawners (Table 4) and smaller values for exploitation rate (Table 11) have resulted. Therefore, effective fishing effort has actually declined since the 1960's (Fig. 13). The implication is that the increased landings since 1978 are the result of exceptionally good recruitment (i.e., year classes) and not the result of greater fishing effort. Increased availability of gulf menhaden to the fishery does not seem likely, given the loss of reduction plants at the geographic extremes (Table 1) and area and seasonal closures that have been implemented (Christmas et al. 1983).

Although recruitment has been high since the late 1970's, it depends largely upon environmental conditions that are beyond the control of management (as evidenced by the unexplained scatter in Figure 16). To the extent that recruitment does depend upon the spawning stock, the dependency rests primarily on age-2 spawners. The concern to management is that several poor environmental years leading to several poor recruitment years could put the gulf menhaden population at risk. Thus, there is need for frequent monitoring and evaluation of the gulf menhaden stock.

Estimates of MSY data range from 620 to 700 KMT based on surplus production models (landings and fishing effort data from 1946-85 fishing years), and from 705 to 825 KMT based on population simulation models (using Ricker spawner-recruit relationships based on 1964-82 year classes). The latter range of estimates for MSY is probably more indicative of the average landings that could have been removed from the gulf menhaden stock during the period from which data were obtained (1964-85 fishing years), given the limitations in adjusting the fishing effort (restricted to 1964-83 fishing years, Table 11) used in surplus production models and the firmer biological basis for the population simulation approach. The concern is that recent landings greater than historical estimates of MSY (greater than 850 KMT since 1982, Table 2) may be too high. However, these analyses are always retrospective and have an inherent time lag in them which prevents a direct assessment of the period since 1982.

Estimates of MSY from surplus production models continue the upward trend noted in Nelson and Ahrenholz (1986). Chapoton (1972) obtained an estimate of MSY of 430 KMT for the 1946-70 period, Schaaf (1975) obtained an estimate of 478 KMT for the 1946-72 period, and Nelson and Ahrenholz (1986) obtained estimates ranging from 540 to 640 KMT for the 1946-79 period. The primary biological concern raised by stock assessment scientists is that the nature of the descending limb can only be determined accurately if landings exceed the current MSY for several years. If the descending limb were steep, this could put the stock at risk. The Pella-Tomlinson model from catch and effective effort data has a flat descending limb ($m=0.99$, Fig. 14), while the Pella-Tomlinson model from catch and population F data has a steep slope ($m=2.78$).

The gulf menhaden is shorter lived than the Atlantic menhaden (higher natural mortality), which can result in rapid year-to-year changes in fishable stock. Although increasing the number of year classes in the fishable stock is neither biologically practical nor suggested, caution is advised relative to the high F's found and the dependency of the fishery upon very few age groups. Expansion of this fishery by effort or area is not recommended.

In summary, the gulf menhaden fishery is currently fully exploited and biologically 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. Although recent short-term harvests in excess of MSY do not appear detrimental to the stock, long-term harvesting above MSY cannot be maintained given our current understanding of the resource and uncertainties in our estimates of MSY.

Acknowledgments

Thanks are due to the many past and present employees of the Southeast Fisheries Center, Beaufort Laboratory, who were involved in the many aspects of the menhaden program, especially Eldon J. Levi, Ethel A. Hall, and Joseph W. Smith. I am grateful to Charles W. Krouse for his assistance in preparing the computerized data sets for analysis and for other programming help. I would also like to thank Dean W. Ahrenholz for getting me started on several of the computer library programs used in these analyses, my wife Nancy for loading many of the tables and figures on our home microcomputer, and Herbert R. Gordy for final drafting of the figures. I thank Dean W. Ahrenholz, Joseph W. Smith, James R. Waters, Charles S. Manooch, John V. Merriner, and two anonymous reviewers for reviewing this manuscript.

Citations

ABRAMSON, N. J.
1971. Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101:1-154.

AHRENHOLZ, D. W.
1981. Recruitment and exploitation of gulf menhaden (*Brevoortia patronus*). Fish. Bull., U.S. 79:325-335.

BEVERTON, R. J. H., and S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II Mar. Fish. G.B. Minist. Agric. Fish. Food 19:533 p.

CHAPOTON, R. B.
1972. The future of the gulf menhaden, the United States' largest fishery. Proc. Gulf Caribb. Fish. Inst. 24:134-143.

CHESTER, A. J.
1984. Sampling statistics in the Atlantic menhaden fishery. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 9, 16 p.

CHRISTMAS, J. Y., and D. J. ETZOLD.
1977. The menhaden fishery of the Gulf of Mexico, United States: A regional management plan. Gulf Coast Res. Lab. Tech. Rep. Ser. 1, 53 p.

CHRISTMAS, J. Y., D. J. ETZOLD, and L. B. SIMPSON.
1983. The menhaden fishery of the Gulf of Mexico, United States: A regional plan. Gulf States Mar. Fish. Comm. 8, 107 p.

CLARK, C. W., and M. MANGEL.
1979. Aggregation and fishery dynamics: A theoretical study of schooling and the purse seine tuna fisheries. Fish. Bull., U.S. 77:317-337.

EPPERLY, S. P., W. H. LENARZ, L. L. MASSEY, and W. R. NELSON.
1986. A generalized computer program for yield per recruit analysis of a migrating population with area specific growth and mortality rates. NOAA Tech. Memo. NMFS-SEFC-180, Southeast Fish. Cent., Natl. Mar. Fish. Serv., Miami, FL 33149, 26 p.

FOX, W. W., Jr.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.
1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. Fish. Bull., U.S. 73:23-37.

LENARZ, W. H., W. W. FOX, Jr., G. T. SAKAGAWA, and B. J. ROTHSCHILD.
1974. An examination of the yield per recruit basis for a minimum size regulation for Atlantic yellowfin tuna, *Thunnus albacares*. Fish. Bull., U.S. 72:37-61.

LEWIS, R. M., and C. M. ROITHMAYR.
1981. Spawning and sexual maturity of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 78:947-951.

MURPHY, G. I.
1965. A solution of the catch equation. J. Fish. Res. Board Can. 22:191-201.

NELSON, W. R., and D. W. AHRENHOLZ.
1986. Population and fishery characteristics of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 84:311-325.

NICHOLSON, W. R.
1978. Gulf menhaden, *Brevoortia patronus*, purse seine fishery: Catch, fishing activity, and age and size composition, 1964-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 722,9 p.

NICHOLSON, W. R., and W. E. SCHAAF.
1978. Aging of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 76:315-322.

PELLA, J. J., and P. K. TOMLINSON.
1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. 14:420-496.

REISH, R. L., R. B. DERISO, D. RUPPERT, and R. J. CARROLL.
1985. An investigation of the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*). Can. J. Fish. Aquat. Sci. 42:147-157.

RICKER, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

SCHAAF, W. E.
1975. Status of the gulf and Atlantic menhaden fisheries and implications for resource management. Mar. Fish. Rev. 37(9):1-9.

SCHAEFER, M. B.
1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 1:27-56.
1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 2:247-268.

TOMLINSON, P. K.
1970. A generalization of the Murphy catch equation. J. Fish. Res. Board Can. 27:821-825.

ULLTANG, O.
1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). J. Cons. Cons. Int. Explor. Mer 37:249-260.

VAUGHAN, D. S., and P. KANCIRUK.
1982. An empirical comparison of estimation procedures for the von Bertalanffy growth equation. J. Cons. Cons. Int. Explor. Mer 40:211-219.

VAUGHAN, D. S., R. M. YOSHIYAMA, J. E. BRECK, and D. L. DEANGELIS.
1984. Modeling approaches for assessing the effects of stress on fish populations. In Cairns, V. W., P. V. Hodson, and J. O. Nriagu (eds.), Contaminant effects on fisheries, p. 259-278. Wiley, New York.

VON BERTALANFFY, L.
1938. A quantitative theory of organic growth. Human Biol. 10:181-213.

WALTERS, C. J.
1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98:505-512.