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Gulf menhaden (*Brevoortia patronus*) in the U.S. Gulf of Mexico: Fishery characteristics and biological reference points for management

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Abstract

Gulf menhaden, *Brevoortia patronus*, plays a key ecological role in the northern Gulf of Mexico and supports the second largest commercial fishery by weight in the United States. Here we describe that fishery and propose biological reference points (BRPs) for its management. The BRPs represent targets and limits of both fishing mortality rate (F) and population fecundity (Ψ), where *target* is defined as the management goal, and *limit*, a value to be avoided ($F < F_{\mathrm{Limit}}$ and $\Psi > \Psi_{\mathrm{Limit}}$). We assess stock status relative to the BRPs by fitting a statistical catch-age model to fishery-dependent and fishery-independent data spanning 1964–2004. Results indicate that in the terminal year neither limit reference point is exceeded ($F_{2004}/F_{\mathrm{Limit}} = 0.75$ and $\Psi_{2004}/\Psi_{\mathrm{Limit}} = 1.86$). Of possible concern, however, is a recent increase in fishing mortality and decrease in population fecundity. With these trends, terminal values exceed their targets ($F_{2004}/F_{\mathrm{Target}} = 1.16$ and $\Psi_{2004}/\Psi_{\mathrm{Target}} = 0.93$), although by little relative to uncertainty in the estimates. Sensitivity analyses show these results are robust to model assumptions.
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Keywords: Biological reference points; *Brevoortia patronus*; Fishery management; Gulf menhaden; Stock assessment

1. Introduction

Gulf menhaden, *Brevoortia patronus*, is a small (generally <22 cm fork length), euryhaline clupeid fish found in coastal waters of the northern Gulf of Mexico (Nelson and Ahrenholz, 1986; Christmas et al., 1988). The species ranges from Cape Sable, Florida to Veracruz, Mexico (Reintjes, 1969), although it is most abundant from the Florida Panhandle to eastern Texas. During spring through fall, gulf menhaden form dense, near-surface schools, which are exploited by a large, industrial purse-seine fishery.

As obligate filter feeders, menhaden strain plankton and detritus through an elaborate network of gill rakers attached to the branchial basket (Friedland, 1985). Menhaden themselves are a principal forage food for piscivorous fishes, sea birds, and marine mammals (Ahrenholz, 1991), thus providing a key link between primary producers and secondary consumers.

Although no major longitudinal migrations are known to occur (Pristas et al., 1976; Ahrenholz, 1981), gulf menhaden tend to move inshore in early spring and up to 80 km offshore in late fall (Roithmayr and Waller, 1963). Spawning occurs October through March and peaks offshore in December and January (Lewis and Roithmayr, 1981). Eggs hatch at sea, and larvae are carried by currents to inland waters, where they metamorphose into juveniles. Gulf menhaden spend their first summer in estuaries, then migrate offshore by late fall. The following spring, they move back into coastal waters.

The gulf menhaden fishery dates to the late 1800s (Nicholson, 1978). Records prior to World War II are fragmentary, but annual landings during 1918–1944 probably ranged 2000–12,000 t (Nicholson, 1978). For the 1948 fishing season, Nicholson (1978) documented landings of 103,000 t. Chapoton (1970, 1971) cited a general trend of increased landings from the late 1940s through 1970, noting a peak of 521,500 t in 1969. Landings continued to increase through the 1970s and 1980s, exceeding 800,000 t for six consecutive years (1982–1987) and culminating at 982,800 t in 1984 (Smith, 1991). Since 1988, landings have ranged from 421,400 t (1992) to 761,600 t (1994), showing no apparent trends (Table 1). With current landings of 468,736 t (2004) comprising 11% of all U.S. landings, gulf menhaden supports the second largest commercial fishery in the United States (NMFS, 2005).

The fishery is conducted by a fleet of large (up to 60 m) purse-seine vessels from ports in Mississippi and Louisiana (Smith,

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Table 1
Number of plants, number of vessels, nominal fishing effort of the reduction fishery (vessel-tonne-weeks, v-t-wks), landings, and effective sample size, 1964–2004

Fishing year	No. of reduction plants	No. of vessels	Nominal effort (1000 v-t-wks)	Landings of reduction fishery (1000 t)	Nominal catch/effort of reduction fishery	Landings of bait fishery (1000 t)[a]	Total landings (1000 t)	Effective sample size, n_t (no. fish/10)[b]
1964	11	78	272.9	407.8	1.49	1.2	409.0	613
1965	13	87	335.6	461.2	1.37	1.2	462.4	759
1966	13	92	381.3	357.6	0.94	1.2	358.8	621
1967	13	85	404.7	316.1	0.78	1.2	317.3	703
1968	14	78	382.8	371.9	0.97	1.2	373.1	764
1969	13	75	411.0	521.5	1.27	1.2	522.7	738
1970	13	76	400.0	545.9	1.36	1.2	547.1	520
1971	13	85	472.9	728.5	1.54	1.2	729.7	383
1972	11	75	447.5	501.9	1.12	1.2	503.1	989
1973	10	66	426.2	486.4	1.14	1.2	487.6	895
1974	10	71	485.5	587.4	1.21	1.2	588.6	1009
1975	11	78	538.0	542.6	1.01	1.2	543.8	953
1976	11	82	575.8	561.2	0.97	1.2	562.4	1339
1977	11	80	532.7	447.1	0.84	1.2	448.3	1490
1978	11	80	574.3	820.0	1.43	1.2	821.2	1294
1979	11	78	533.9	777.9	1.46	1.2	779.1	1112
1980	11	79	627.6	701.3	1.12	1.0	702.3	988
1981	11	80	623.0	552.6	0.89	1.1	553.7	1027
1982	11	82	653.8	853.9	1.31	1.6	855.5	1034
1983	11	81	655.8	923.5	1.41	1.7	925.2	1452
1984	11	81	645.9	982.8	1.52	2.3	985.1	1594
1985	7	73	560.6	881.1	1.57	3.0	884.1	1323
1986	8	72	606.5	822.1	1.36	8.5	830.6	1649
1987	8	75	604.2	894.2	1.48	17.3	911.5	1646
1988	8	73	594.1	623.7	1.05	16.0	639.7	1240
1989	9	77	555.3	569.6	1.03	13.5	583.1	1395
1990	9	75	563.1	528.3	0.94	11.1	539.4	1146
1991	7	58	472.3	544.3	1.15	8.6	552.9	1138
1992	6	51	408.0	421.4	1.03	10.9	432.3	1421
1993	6	52	455.2	539.2	1.18	12.0	551.2	1458
1994	6	55	472.0	761.6	1.61	9.9	771.5	1606
1995	6	52	417.0	463.9	1.11	8.1	472.0	1349
1996	5	51	451.7	479.4	1.06	9.0	488.4	1212
1997	5	52	430.2	611.2	1.42	8.8	620.0	992
1998	5	50	409.3	486.2	1.19	10.0	496.1	904
1999	5	55	414.5	684.3	1.65	9.8	694.1	1064
2000	4	47	417.6	579.3	1.39	4.3	583.6	838
2001	4	44	400.6	521.3	1.30	6.4	527.7	622
2002	4	43	386.7	574.5	1.49	7.5	582.0	560
2003	4	42	363.2	517.1	1.42	6.6	523.7	784
2004	4	42	390.5	468.7	1.20	4.5	473.2	664

[a] Average bait landings in 1980–1982 are used to represent the small amount of unknown bait landings in 1964–1979. Bait landings in 2004 are preliminary, as they do not include the typically trivial amount of landings from November to December.
[b] Sample size in 1964–1971 was 20 fish, thus n_t for the period was no. fish/20.

1991). Coastal in nature, the fishery harvests up to 93% of its catch from within 16 km of the shoreline (Smith et al., 2002). One Gulf Coast state, Louisiana, dominates the harvest, with up to 92% of the annual catch in recent years. Shore-side reduction factories process the fish into meal, oil, and soluble products. In addition, a small purse-seine fishery for gulf menhaden as bait exists in Louisiana, but its landings are dwarfed by those of the reduction fishery.

Management of the fishery is by interstate agreement through the Gulf States Marine Fisheries Commission (Vanderkooy and Smith, 2002). The fishing season extends from the third Monday in April through November 1. Purse-seining for menhaden has been prohibited by Florida since 1995 and by Alabama since 2003, but remains legal with restrictions in territorial waters of Mississippi, Louisiana, and Texas (Vanderkooy and Smith, 2002).

Historically, up to 14 reduction plants (in 1968, Table 1) processed gulf menhaden (Nicholson, 1978), but the number of plants stabilized at 11 in 1975–1984 (Smith et al., 1987). Several ports, such as Cameron, Empire, and Moss Point, supported multiple factories owned by various companies. Beginning in 1985, corporate acquisitions and company downsizing reduced the number of menhaden processing facilities to eight by 1986, six by 1992, and four by 2000 (Vanderkooy and Smith, 2002). Since 2000, a single company has dominated the fishery, operating three of the four extant plants in the northern Gulf.

Commensurate with the decline in fish plants has been the reduction in number of gulf menhaden purse-seine vessels. Fleet size peaked at 82 vessels in 1982 (Vanderkooy and Smith, 2002). Several downsizings followed: to 73 vessels in 1985, to 58 vessels in 1991, and to 47 vessels in 2000 (Table 1). In 2004, 41 vessels unloaded gulf menhaden for reduction at four Gulf ports (Abbeville, Cameron, Empire, and Moss Point).

Nominal or observed fishing effort in the gulf menhaden fishery is measured in vessel-tonne-weeks (v-t-wks), defined as a vessel's net tonnage times the number of weeks that vessel unloaded fish at least one day (Smith, 1991). Nominal effort peaked at 655,800 v-t-wks in 1983, the year prior to peak landings. In general, observed landings have tracked effort over the past four decades (Table 1).

Capture of gulf menhaden for use as bait has constituted only a small fraction of total landings (Vanderkooy and Smith, 2002). Bait landings occurred almost exclusively in Florida (mainly from Tampa Bay and the Panhandle areas) until the late 1980s, when Louisiana and Alabama began landing substantial quantities. Louisiana became the principal state for bait landings after Florida banned most commercial net gear in 1995. Landings for bait peaked at about 17,000 t in the late 1980s, and since the 1990s, have averaged about 9000 t annually (Table 1).

The U.S. National Marine Fisheries Service has monitored the gulf menhaden fishery since 1964, collecting information on daily landings, nominal fishing effort, and size and age compositions of the catch (Nicholson, 1978; Smith et al., 1987). Here we use these data and others to assess status of the stock and fishery. Previous stock assessments have summarized fishery-dependent data from earlier decades (Nelson and Ahrenholz, 1986; Vaughan, 1987; Vaughan et al., 1996, 2000). This assessment is the first to include a fishery-independent index of abundance and to propose biological reference points for managing the economically and ecologically important stock of gulf menhaden.

2. Methods

To assess the status of gulf menhaden, we developed a statistical catch-age model (Deriso et al., 1985; Quinn and Deriso, 1999), fit to data from the fishery and from fishery-independent surveys. The model provided estimates of population fecundity and age-specific fishing mortality rates for 1964–2004. We compared those values to target and limit reference points to estimate status of stock and fishery.

2.1. Fishery data

Daily vessel unloads are reported monthly to the National Marine Fisheries Service. Sampling error in landings, as measured by the coefficient of variation (CV), has been estimated[1] to be about 4%. Landings for bait are generally monitored by state agencies. Since 1980, bait landings have averaged about 1.2% of the total menhaden landings (Vanderkooy and Smith, 2002). Rather than treating bait and reduction landings as separate, we combined them into a single time series.

Biostatistical sampling of the reduction fishery is based on a two-stage, cluster design, applied since 1964 across the geographic and temporal range of the fishery (Chester, 1984). The first cluster represents the number of vessels (or purse-seine sets), and the second cluster represents fish sampled per vessel. Under current protocol, a port agent randomly selects a vessel at dockside, and then randomly selects 10 fish (20 in 1964–1971) from the top of the fish hold. Each of these fish is measured for fork length (mm) and weight (g), and a scale patch is removed for ageing (Nicholson and Schaaf, 1978). The sample is not assumed to represent the entire fish hold, but rather the last purse-seine set of the fishing day. In recent years, about 6700 fish have been processed annually. Typically, 90% or more of the annual catch consists of age-1 and age-2 gulf menhaden (Nicholson, 1978; Smith et al., 1987). At the end of the fishing season, biostatistical data are merged with landings on a port-week basis to produce estimated landings at age (in numbers). Estimates are summed over all port-weeks for the entire fishing season to produce annual estimates of total landings at age (Table 2). These annual estimates were treated as data for fitting the assessment model.

2.2. Fishery-independent index of juvenile abundance

We developed an index of juvenile abundance using catch-per-unit-effort data collected by field biologists in Mississippi, Louisiana, and Texas. (No index of adult abundance could be developed, as adult menhaden are not well represented in any fishery-independent surveys.) Sampling methods varied by state. In Mississippi[2], data were collected 1974–2004 using 16-ft trawl, 50-ft bag seine, and beam plankton net; in Louisana, data were collected 1967–2004 using otter trawls (Perret et al., 1971); in Texas, data were collected 1978–2004 using bag seines (Martinez-Andrade et al., 2005). Analyses were restricted to data from primary sampling months of each survey (February through July for Mississippi, January through July for Louisana, and March through September for Texas).

Data were scaled using a two-step process. First, catch-per-unit-effort data from each gear were standardized to their means. Second, these standardized values were weighted by state according to area and productivity of streams across the northern Gulf of Mexico, as estimated by Ahrenholz et al. (1989). The applied weights represented each state's contribution to total juvenile abundance: 1.9% for Mississippi, 52.2% for Louisiana, and 45.9% for Texas. Standardized values of catch-per-unit-effort from each state were multiplied by that state's proportional contribution.

These data were combined into a single, coast-wide index via a generalized linear model (Hardin and Hilbe, 2001). The

[1] Kutkuhn, J.H. 1966. Verification of menhaden conversion factor. Unpublished report. NOAA Beaufort Laboratory, 4 pp.

[2] Unpublished data, Monitoring and Assessment of Mississippi's Interjurisdictional Marine Resources, Gulf Coast Research Laboratory, University of Southern Mississippi, October 1973–present.

Table 2
Estimated catch in numbers at age (in million fish) from the gulf menhaden reduction fishery, 1964–2004

Year	0	1	2	3	4	5	6	Total
1964	2.8	3329.3	1495.2	118.1	4.4	0.0	0.0	4949.6
1965	43.4	5031.4	1076.6	80.3	0.7	0.0	0.0	6232.4
1966	30.5	3314.4	865.2	33.8	0.3	0.0	0.0	4244.1
1967	22.4	4267.7	337.7	13.0	0.0	0.0	0.0	4640.8
1968	65.1	3475.2	1001.3	37.5	0.5	0.0	0.0	4579.5
1969	20.8	6075.0	1286.3	31.7	0.0	0.0	0.0	7413.8
1970	50.2	3279.9	2280.0	36.1	0.0	0.0	0.0	5646.1
1971	21.6	5761.1	1955.5	181.8	4.1	0.0	0.0	7924.1
1972	19.1	3047.7	1733.5	88.5	4.0	0.0	0.0	4893.0
1973	49.9	3033.0	1107.0	99.6	1.3	0.0	0.0	4290.8
1974	1.4	3846.8	1471.7	59.1	0.0	0.0	0.0	5378.9
1975	108.8	2440.5	1499.2	461.8	0.2	0.0	0.0	4510.5
1976	0.0	4591.4	1373.9	203.9	0.0	0.0	0.0	6169.3
1977	0.0	4660.0	1331.7	110.4	5.6	0.0	0.0	6107.7
1978	0.0	6787.4	2742.0	52.7	5.2	0.0	0.0	9587.4
1979	0.0	4701.2	2877.2	337.2	6.1	0.8	0.0	7922.4
1980	65.9	3409.4	3261.1	436.2	46.3	1.6	0.0	7220.4
1981	0.0	5750.5	1424.9	329.4	29.7	3.3	1.2	7539.1
1982	0.0	5146.7	3302.0	503.5	58.5	2.1	1.7	9014.5
1983	0.0	4685.7	3809.2	382.6	23.8	1.3	0.0	8902.7
1984	0.0	7749.6	2881.5	438.4	49.0	0.7	0.0	11119.2
1985	0.0	8682.7	2498.6	233.7	36.5	0.0	0.0	11451.6
1986	0.0	4276.0	4892.0	174.9	25.8	1.0	0.0	9369.7
1987	0.0	6699.5	3975.6	427.8	12.5	0.0	0.0	11115.3
1988	0.0	5337.7	2581.4	151.5	18.0	0.0	0.0	8088.5
1989	0.0	5550.4	1622.0	67.0	2.1	0.0	0.0	7241.5
1990	0.0	3889.2	1785.0	136.2	13.1	0.3	0.4	5824.4
1991	0.0	2217.5	2339.9	215.6	28.2	2.5	0.0	4803.7
1992	0.0	2187.3	1505.8	197.1	24.2	1.7	0.2	3916.2
1993	0.0	3492.8	1532.9	193.5	15.7	2.8	0.2	5237.9
1994	0.0	3627.6	3195.6	441.2	49.0	3.7	0.0	7317.0
1995	0.0	1369.2	2423.4	99.7	3.9	0.2	0.0	3896.3
1996	0.0	1784.2	2513.7	251.1	16.8	0.9	0.0	4566.8
1997	0.0	3235.6	2398.8	276.1	38.2	1.3	0.0	5950.0
1998	0.0	1804.8	2587.1	189.7	15.2	1.6	0.0	4598.4
1999	0.0	3368.8	2393.0	416.9	19.7	0.0	0.0	6198.3
2000	0.0	2029.8	3164.5	347.7	62.5	3.4	0.0	5607.9
2001	0.0	987.7	2654.2	290.2	18.9	0.8	0.0	3951.7
2002	0.0	1585.6	2863.1	534.0	17.1	0.0	0.0	4999.8
2003	0.0	1910.1	3011.7	339.6	13.4	0.0	0.0	5274.7
2004	0.0	2799.4	1764.0	400.3	37.6	0.0	0.0	5001.3

model's explanatory variables were year, month, area, and gear; and the response variable – catch-per-unit-effort – was assumed distributed with delta-lognormal error structure (Lo et al., 1992; Maunder and Punt, 2004). This structure models the proportion of positive catches with binomial error, and catch-per-unit-effort of successful trips with lognormal error. Annual coefficients of variation were estimated by empirical bootstrap with 1000 replicates (Efron and Tibshirani, 1993).

2.3. Life-history information

The assessment model included life-history information on growth, maturity, fecundity, and natural mortality. We modeled growth in fork length using the von Bertalanffy equation, with year-specific parameters estimated from biostatistical data of the reduction fishery. Using these same data, we estimated year-specific parameters (α_t and β_t) of the weight–length relationship, $w_{a,t} = \alpha_t l_{a,t}^{\beta_t}$, where $w_{a,t}$ is weight (g) at age and $l_{a,t}$ is fork length (mm) at age in the middle of year t. Although length and weight at age varied annually, they showed no particular trends across years.

Maturity and fecundity information were provided by Lewis and Roithmayr (1981). Maturity at age was estimated to be knife-edge, with full maturity occurring at age-2 (Table 3). Annual fecundity at age ($\psi_{a,t}$) was computed from length at age, $\psi_{a,t} = 0.0000516 \times l_{a,t}^{3.8775}$, using lengths at the beginning of each calendar year.

Age-specific natural mortality rates (M_a) were assumed to decline with increasing weight, following the method of Boudreau and Dickie (1989). These age-specific rates were then scaled to adult natural mortality using estimates from tagging data (Ahrenholz, 1981). Ahrenholz (1981) reported a mean, upper, and lower estimate of adult natural mortality (Table 3).

Table 3
Age-specific natural mortality rate and proportion of mature females

Age	Natural mortality rate				Proportion females mature	
	Scaled to lower value	Scaled to mean value	Scaled to upper value	Constant	Knife-edge	Gradual
0	1.34	2.10	3.06	1.10	0.00	0.00
1	0.97	1.53	2.23	1.10	0.00	0.20
2	0.81	1.27	1.84	1.10	1.00	1.00
3–6+	0.70	1.10	1.60	1.10	1.00	1.00

Base model used natural mortality rate scaled to mean value and knife-edge female maturity. Age-dependent natural mortality rates estimated using the method of Boudreau and Dickie (1989), rescaled to tagging estimates from Ahrenholz (1981).

2.4. Assessment model

The statistical catch-age model (detailed in Table 4) was fit by maximum likelihood to the data—juvenile abundance index, fishery landings, and age compositions—beginning in 1964, the first year of biostatistical sampling. Estimated quantities included a spawner–recruit relationship, a scaling parameter of the juvenile abundance index, fishery selectivities, annual fishing mortality rate, and annual population fecundity. Separate selectivities were estimated for two periods, 1964–1975 and 1976–2004, to account for an apparent change in the fishery. As recognized by Vaughan et al. (1996), the catch matrix in the earlier period comprised age classes 0–3, and in the later period, age classes 1–4+. This shift may have occurred due to changes in ageing techniques, mesh size, or fishing locations.

The spawner–recruit relationship was quantified using the Beverton–Holt model (Beverton and Holt, 1957) with lognormal deviation to predict recruitment from population fecundity. In many assessments, reliable information on population fecundity is unavailable, and spawning stock biomass gets used in its place, under the evidence or assumption that egg production scales linearly with body weight. When it does not, use of spawning stock biomass introduces error to the spawner–recruit model (Rothschild and Fogarty, 1989). In gulf menhaden, egg production at age increases more quickly than body weight at age, and thus spawning stock biomass would underplay reproductive capacity. This source of error was avoided altogether, by using population fecundity directly.

Uncertainty in estimates of management quantities—fishing mortality rate and population fecundity—was computed from the inverse Hessian matrix. This approach is common in assessment models fit by maximum likelihood (Booth and Quinn, 2006). It assumes that parameter values are asymptotically normally distributed and does not include uncertainty in model specification.

We defined a base model assuming knife-edge maturity (Table 3), mean natural mortality (Table 3), and the Beverton–Holt spawner–recruit relationship. Effects of these assumptions and retrospective error on estimated stock status were examined via sensitivity and retrospective analyses.

2.5. Sensitivity and retrospective analyses

Sensitivity and retrospective analyses were implemented as variations of the base model. Sensitivity analyses were used to quantify the influences of biological inputs, including the spawner–recruit relationship (Beverton–Holt or Ricker), the natural mortality schedule (M_a scaled high, medium, or low; or constant across age), and the maturity schedule (knife-edge or gradual). Retrospective analyses were used to quantify potential error in terminal-year estimates (Cadrin and Vaughan, 1997), examined by sequentially truncating the last year of data (2003, 2002, 2001, 2000). Overall, we fit 10 different models (Table 5) to estimate status of stock and fishery.

2.6. Biological reference points

Biological reference points are benchmarks against which to measure stock or fishery status. They usually serve as targets or limits, where a target represents a long-term management goal, and a limit is a value to be avoided. The distance between target and limit acts as a buffer to prevent frequent overexploitation.

Reference points have not previously been applied to management of gulf menhaden. We therefore propose target and limit reference points, based here on per recruit analysis (Sissenwine and Shepherd, 1987; Gabriel et al., 1989; Caddy and Mahon, 1995). Per-recruit reference points have been found useful proxies for MSY-based values when the spawner–recruit relationship shows considerable noise, as with gulf menhaden (Vaughan et al., 2000).

The proposed reference points (Table 4) are similar to those used for management of Atlantic menhaden (ASMFC, 2004). They represent targets and limits of fishing mortality rate and population fecundity. (We use the term *population fecundity* synonymously with *total egg production*.) Following ASMFC (2004), we computed the fishing mortality target (F_{Target}) as the fishing mortality rate corresponding to the 75th percentile of annual fecundity potential ratio (FPR), defined as equilibrium fecundity per recruit relative to that at $F = 0$. Likewise, we computed the fishing mortality limit (F_{Limit}) as the fishing mortality rate corresponding to the median of annual FPR. Thus, F_{Limit} is analogous to the common limit reference point F_{med}, also called F_{rep}, defined as the fishing mortality rate with stock replacement in 50% of years (Sissenwine and Shepherd, 1987; Caddy and Mahon, 1995). Given these percentiles (75th or median) of annual FPR, values of F were calculated from a single FPR curve that assumed mean egg production. We then computed the population fecundity target (Ψ_{Target}) as the median fecundity per recruit multiplied by the median annual recruitment, and the population fecundity limit (Ψ_{Limit}) as one-half of Ψ_{Target} (Restrepo

Table 4
General descriptions and definitions of the catch-age model

Definition	Symbol	Description or equation
General		
Index of years	t	$t=\{1958, \ldots, 2004\}$, including an initialization period (1958–1963) prior to the first year of data (1964)
Index of time periods	t'	$t'=\{1, 2\}$, where 1 represents 1964–1975 and 2 represents 1976–2004
Index of ages	a	$a=\{0, \ldots, A\}$, where $A=6+$
Input data		
Weight at age	$w_{a,t}$	Annual mean weight (g) at age of fish landed in year t (midpoint of year)
Maturity at age	m_a	Proportion of individuals mature at age a
Eggs at age	$\psi_{a,t}$	Eggs produced per individual at age a in year t
Observed index of juvenile abundance	U_t	Based on delta-lognormal model applied to data from LA, MS, and TX
Coefficient of variation of U_t	c_t^U	Estimated by bootstrap ($N=1000$) of delta-lognormal model
Observed landings	L_t	Reported landings in weight (1000 t) from reduction and bait fisheries combined
Coefficient of variation of L_t	c_t^L	Assumed $c_t^L=0.04$ for all years
Observed age compositions	$p_{a,t}$	Proportion of individuals at age a in year t from the reduction fishery
Effective sample sizes of age compositions	n_t	Number of samples in year t
Age-dependent natural mortality rate	M_a	Based on the method of Boudreau and Dickie (1989), rescaled according to results of Ahrenholz (1981)
Population model		
Fishery selectivity	$s_{a,t'}$	$s_{a,t'}=1/(1+\exp\{-\hat{\eta}_{t'}(a-\hat{\alpha}_{t'})\})$
Fishing mortality rate	$F_{a,t}$	$F_{a,t}=s_{a,t}\hat{F}_t$, where $\hat{F}_t$ are estimated, fully selected fishing mortality rates and $s_{a,t}=s_{a,t'}$ for t in years represented by t'. In the initialization period, $F_t=F_{1964}$ and $s_{a,t}=s_{a,t'=1}$
Total mortality rate	$Z_{a,t}$	$Z_{a,t}=M_a+F_{a,t}$
Eggs per recruit at $F=0$	$\phi_{0,t}$	$\phi_{0,t}=\sum_a 0.5N'_a m_a\psi_{a,t}$, where N'_a is number per recruit at age a according to the stable age structure under natural mortality alone
Population fecundity	Ψ_t	$\Psi_t=\sum_a 0.5N_{a,t}m_a\psi_{a,t}$, where $0.5N_{a,t}$ is abundance of females at age in year t, assuming a 50:50 sex ratio
Abundance at age in initial year (1958)	$N_{a,t}$	$N_{a+1,1958}=N_{a,1958}\exp(-Z_{a,1958})$, $N_{A,1958}=N_{A-1,1958}\exp(-Z_{A-1,1958})/[1-\exp(-Z_{A,1958})]$, where $\hat{N}_{0,1958}$ is estimated initial recruitment
Abundance at age in other years (1959–2004)	$N_{a,t}$	$N_{0,t}=0.8\hat{R}_0\hat{h}\Psi_t/[0.2\hat{R}_0\phi_{0,t}(1-\hat{h})+(\hat{h}-0.2)\Psi_t]+\hat{\varepsilon}_t$, $N_{a+1,t+1}=N_{a,t}\exp(-Z_{a,t})$, $N_{A,t+1}=N_{A-1,t}\exp(-Z_{A-1,t})+N_{A,t}\exp(-Z_{A,t})$, where $\hat{R}_0$ (virgin recruitment) and $\hat{h}$ (steepness) are estimated parameters of the Beverton–Holt spawner–recruit model, and $\hat{\varepsilon}_t$ are estimated residuals of annual recruitment
Predicted catch at age	$C_{a,t}$	$C_{a,t}=(F_{a,t}/Z_{a,t})N_{a,t}[1-\exp(-Z_{a,t})]$
Predicted landings	$\breve{L}_t$	$\breve{L}_t=\sum_a C_{a,t}w_{a.t}$
Predicted age composition	$\breve{p}_{a,t}$	$\breve{p}_{a,t}=C_{a,t}/\sum_a C_{a,t}$
Predicted index of juvenile abundance	$\breve{U}_t$	$\breve{U}_t=\hat{q}N_{0,t}$, where $\hat{q}$ is estimated catchability of age-0 fish
Negative log-likelihood		
Multinomial age composition	Λ_1	$\Lambda_1=-\sum_{t=1964}^{2004}n_t\sum_a p_{a,t}\ln(\breve{p}_{a,t})-p_{a,t}\ln(p_{a,t})$
Lognormal index	Λ_2	$\Lambda_2=\sum_{t=1967}^{2004}[\ln(U_t/\breve{U}_t)]^2/2(c_t^U)^2$
Lognormal landings	Λ_3	$\Lambda_3=\sum_{t=1964}^{2004}[\ln(L_t/\breve{L}_t)]^2/2(c_t^L)^2$
Recruitment constraint	Λ_4	$\Lambda_4=\sum_{t=1959}^{2004}(\hat{\varepsilon}_t)^2$
Total log-likelihood	Λ	$\Lambda=\sum_{i=1}^{4}\Lambda_i$, objective function minimized by the assessment model
Biological reference points		
Annual fecundity per recruit	ϕ_{F_t}	$\phi_{F_t}=\sum_a 0.5N'_a m_a\psi_{a,t}$, where N'_a is the number per recruit at age a according to the stable age structure under $Z_{a,t}$
Annual fecundity potential ratio	Φ_t	$\Phi_t=\phi_{F_t}/\phi_{0,t}$
Curve of mean fecundity potential ratio	$\Phi_\mu(F)$	Fecundity potential ratio as a function of F. Based on mean egg production $\bar{\psi}_a$, computed from period $t'=2$
Fishing mortality target	F_{Target}	F from $\Phi_\mu(F)$ curve corresponding to the 75th percentile of Φ_t
Fishing mortality limit	F_{Limit}	F on the $\Phi_\mu(F)$ curve corresponding to the median Φ_t
Population fecundity target	Ψ_{Target}	Median ϕ_{F_t} multiplied by median $N_{0,t}$
Population fecundity limit	Ψ_{Limit}	One-half Ψ_{Target}

Hat notation ($\hat{x}$) indicates parameters estimated by the assessment model, and breve notation ($\breve{x}$) indicates computed quantities whose fit to data form the objective function.

Table 5
Base model and sensitivity runs

Model	Egg–recruit function	Terminal year	Natural mortality rate[a]	Proportion females mature[a]
M1 (base)	Beverton–Holt	2004	Mean	Knife-edge
M2	Ricker	2004	Mean	Knife-edge
M3	Beverton–Holt	2004	Upper	Knife-edge
M4	Beverton–Holt	2004	Lower	Knife-edge
M5	Beverton–Holt	2004	Constant	Knife-edge
M6	Beverton–Holt	2004	Mean	Gradual
M7	Beverton–Holt	2003	Mean	Knife-edge
M8	Beverton–Holt	2002	Mean	Knife-edge
M9	Beverton–Holt	2001	Mean	Knife-edge
M10	Beverton–Holt	2000	Mean	Knife-edge

[a] Values shown in Table 3.

et al., 1998). All percentiles were based on annual estimates from the assessment period 1964–2004.

For comparison with the proposed F_{Target} and F_{Limit}, we computed other common reference points, namely $F_{\max}$, $F_{0.1}$, and $F_{\%\mathrm{FPR}}$. Both $F_{\max}$ and $F_{0.1}$ stem from analysis of yield per recruit: $F_{\max}$ maximizes yield per recruit, and $F_{0.1}$ is the F where slope of the yield per recruit curve is 10% of its value at the origin. $F_{\%\mathrm{FPR}}$ is the F that corresponds to a particular FPR expressed as a percentage, %FPR (Goodyear, 1993; Caddy and Mahon, 1995). We chose $F_{45\%}$ and $F_{55\%}$.

3. Results

3.1. Base model

In general, the model fit the data well. Predicted and observed landings were in close agreement (Fig. 1), as were predicted and observed age compositions (Fig. 2). Predicted juvenile abundance did not reproduce all extrema in the index, but did track observed trends (Fig. 3).

Estimated selectivity curves for the two periods showed partial selection of age-1 fish and full selection of age-2+ fish (Fig. 4). In the early period (1964–1975), estimated selection of age-1 fish was approximately 0.31, and in the current period (1976–2004), approximately 0.19.

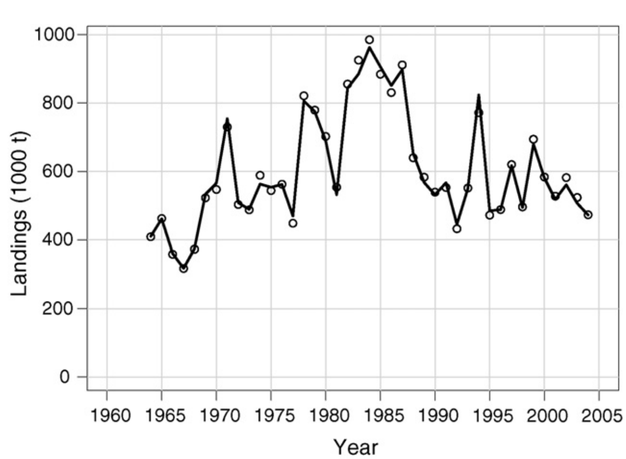

Fig. 1. Observed (circles) and predicted (line) annual landings. Predictions from the base model (M1).

Estimates of fully selected fishing mortality rate were variable prior to 1990, fluctuating between values near $F = 1.0$ and $F > 2.0$ (Fig. 5A). Since 1990, estimates have been lower and less variable, likely effects of industrial consolidation and fleet reduction (Table 1). During the most recent years, estimates have increased from $F = 0.48$ in 2001 to $F = 1.09$ in 2004.

As with F, estimates of population fecundity (Ψ) varied substantially (Fig. 5B). Estimates were lowest in the 1960s, relatively stable in the 1970s and 1980s, generally increasing in the 1990s, and decreasing in the 2000s. After peaking at $\Psi = 165 \times 10^{12}$ in 2000, estimated population fecundity declined to $\Psi = 64 \times 10^{12}$ in 2004. The trends in population fecundity are quite similar to those of age-2+ abundance (figure not shown).

Estimated recruits at age-0 ranged between 74×10^9 (1965) and 542×10^9 (1984) (Fig. 5C). Peaks in estimated recruits occurred two years prior to those in estimated population fecundity, reflecting time to reach maturity. During recent years, estimated recruits have generally declined, from about 464×10^9 in 1998 to 187×10^9 in 2004.

3.2. Sensitivity and retrospective analyses

Choice of spawner–recruit model—Beverton–Holt or Ricker—had little effect on estimated time series (Fig. 5). In retrospect, this result is not surprising, given that the spawner–recruit model was used to generate expected annual recruitment, to which estimated lognormal deviations were added (Table 4). These deviations, lightly constrained, absorbed any potential difference between predictions from the two models.

Models with altered schedules of maturity or natural mortality produced estimated trends similar to those of the base model (Fig. 6). These sensitivity runs, however, displayed notable differences of scale. Estimates of F were inversely related to the magnitude of natural mortality rate. In contrast, estimates of recruits shifted in the same direction as changes in natural mortality of juveniles. Population fecundity reflected those shifts of estimated recruits in the cases of altered natural mortality, and it reflected the presence of age-1 adults in the case of altered maturity.

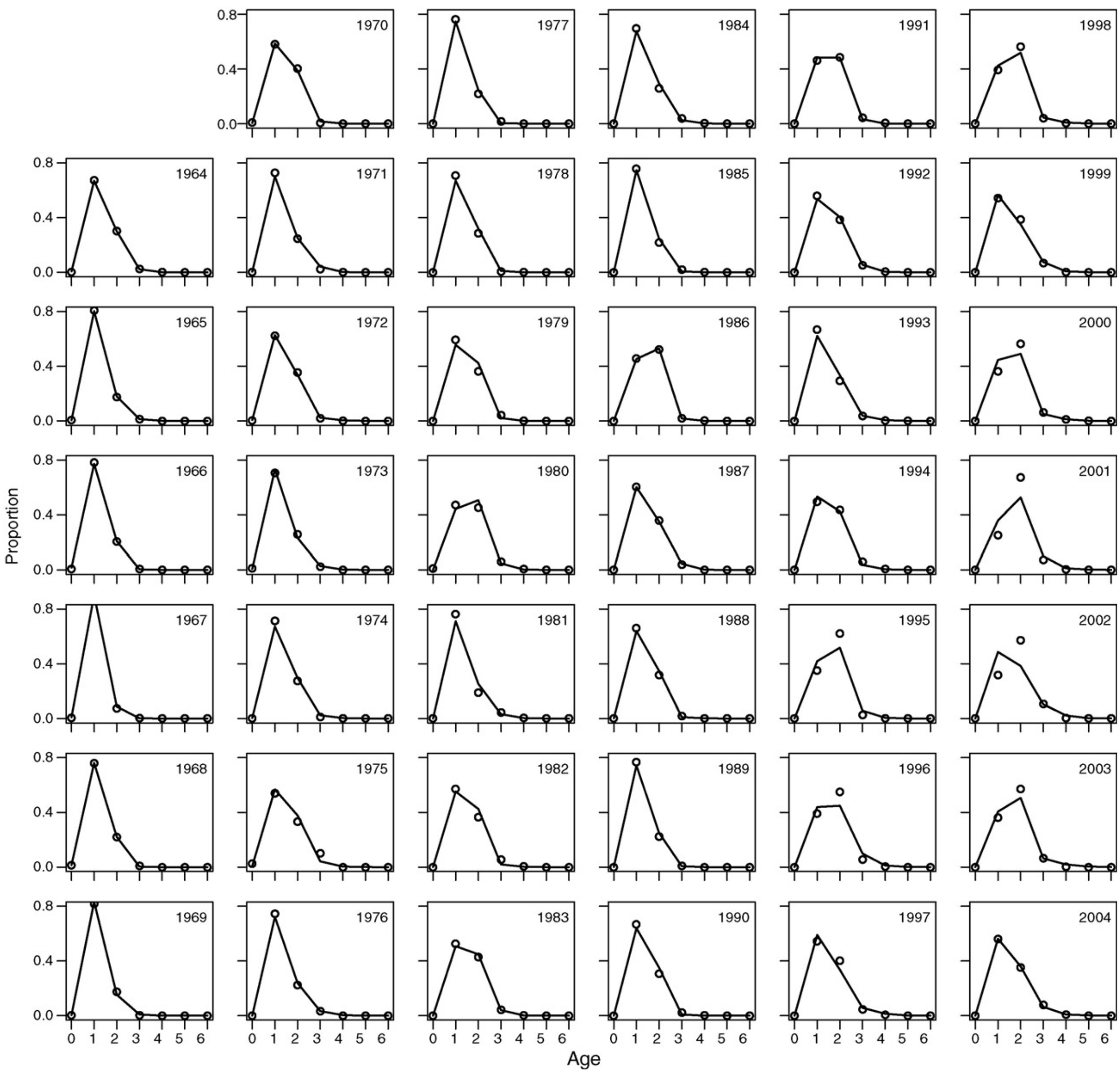

Fig. 2. Observed (circles) and predicted (line) annual age composition of landings. Predictions from the base model (M1).

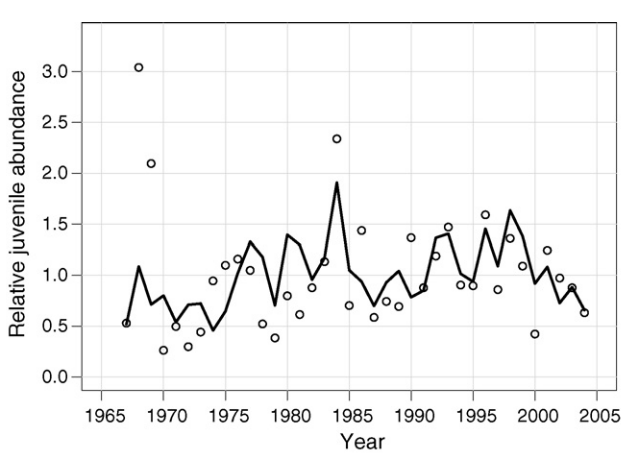

Fig. 3. Observed (circles) and predicted (line) index of juvenile abundance. Predictions from the base model (M1).

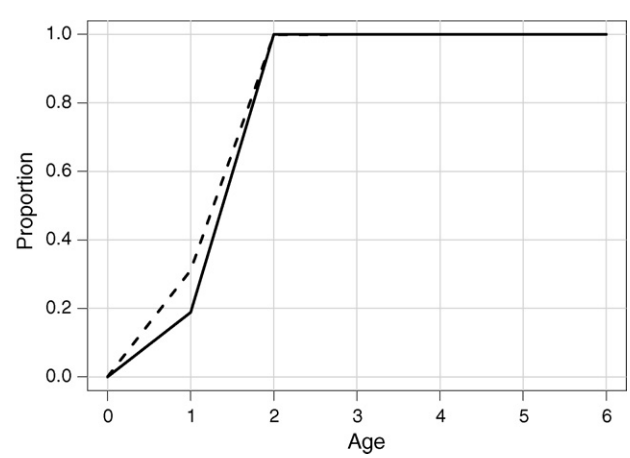

Fig. 4. Estimated selectivity curves from early (1964–1975; dashed) and current (1976–2004; solid) time periods. Estimates from the base model (M1).

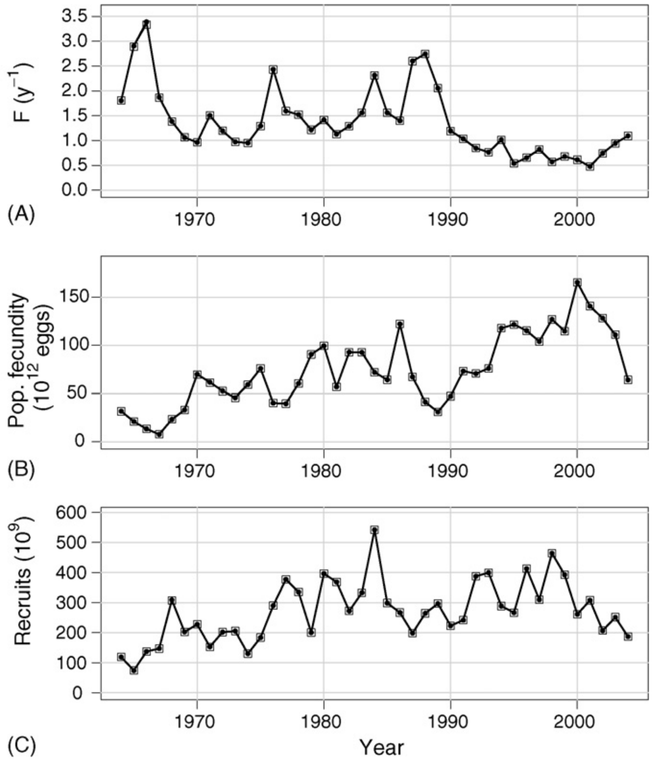

Fig. 5. Estimated time series from the base model (M1; closed circles, bold line) and the model with Ricker recruitment (M2; squares): (A) fully selected fishing mortality rate; (B) population fecundity; and (C) number of age-0 recruits. Estimates from M2 overlay those from M1.

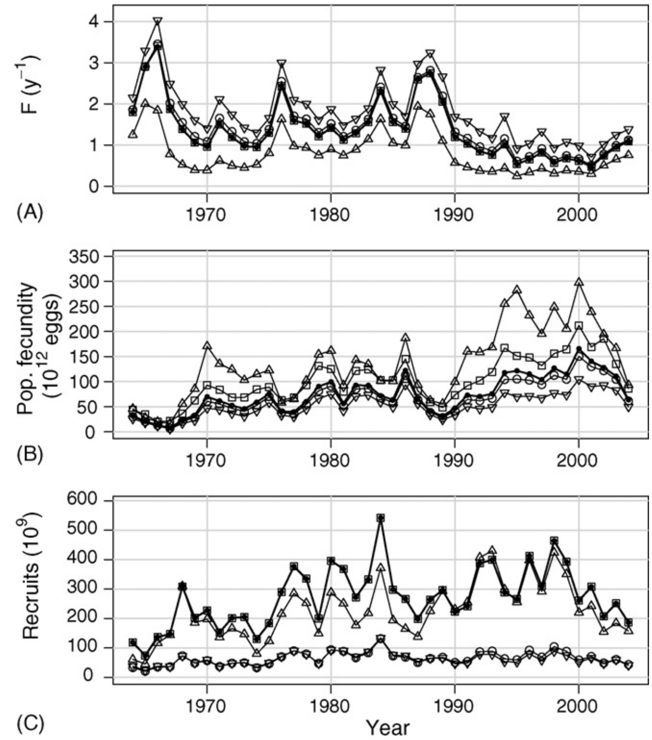

Fig. 6. Estimated time series from the base model (M1; closed circles, bold line) and from models with natural mortality scaled to the upper value (M3; upward triangles), with natural mortality scaled to the lower value (M4; downward triangles), with natural mortality constant (M5; open circles), and with gradual female maturity (M6; squares): (A) fully selected fishing mortality rate; (B) population fecundity; and (C) number of age-0 recruits. In (C), estimates from M3 were divided by 10.

Retrospective analysis revealed some trends in estimation (Fig. 7). Estimates of F tended to be higher in a given year if terminal. Conversely, estimates of population fecundity tended to be lower. These results suggest possible, but small, biases in terminal-year estimates. Estimates of recruits, on the other hand, showed no consistent retrospective pattern, but instead matched precisely the terminal year of the juvenile abundance index. This result occurred because age-0 fish have not yet entered the fishery, and thus data sources other than the index did not influence terminal-year estimates of recruits.

3.3. Biological reference points and fishery status

Biological reference points estimated by the base model were $F_{\text{Target}} = 0.94\ \text{year}^{-1}$, $F_{\text{Limit}} = 1.46\ \text{year}^{-1}$, $\Psi_{\text{Target}} = 68.68 \times 10^{12}$ eggs year^{-1}, and $\Psi_{\text{Limit}} = 34.34 \times 10^{12}$ eggs year^{-1} (Table 6; Fig. 8A). The point estimate of F in the terminal year, $F_{2004} = 1.09$, exceeded its target, indicating that F may need to be reduced (Table 6; Fig. 9). The point estimate of population fecundity in the terminal year, $\Psi_{2004} = 63.91 \times 10^{12}$,

Table 6
Biological reference points estimated by base model and sensitivity runs

Model	Fishing mortality rate (year^{-1})			Population fecundity (10^{12} eggs year^{-1})		
	F_{Target}	F_{Limit}	F_{Terminal}	Ψ_{Target}	Ψ_{Limit}	Ψ_{Terminal}
M1 (base)	0.94	1.46	1.09	68.68	34.34	63.91
M2 (Ricker)	0.94	1.46	1.09	68.67	34.33	63.98
M3 (high M)	0.42	0.71	0.76	134.07	67.04	93.20
M4 (low M)	1.23	1.79	1.38	47.93	23.97	49.85
M5 (constant M)	0.98	1.58	1.12	63.22	31.61	61.34
M6 (gradual maturity)	0.86	1.46	1.09	97.80	48.90	86.22
M7 (retrospective-2003)	0.90	1.47	1.02	68.64	34.32	105.03
M8 (retrospective-2002)	0.93	1.45	1.05	68.96	34.48	108.54
M9 (retrospective-2001)	0.91	1.42	0.94	69.67	34.84	92.73
M10 (retrospective-2000)	0.90	1.40	0.80	69.27	34.64	143.26

Models details are indicated and described more fully in Table 5. Terminal-year estimates are included for comparison to reference points.

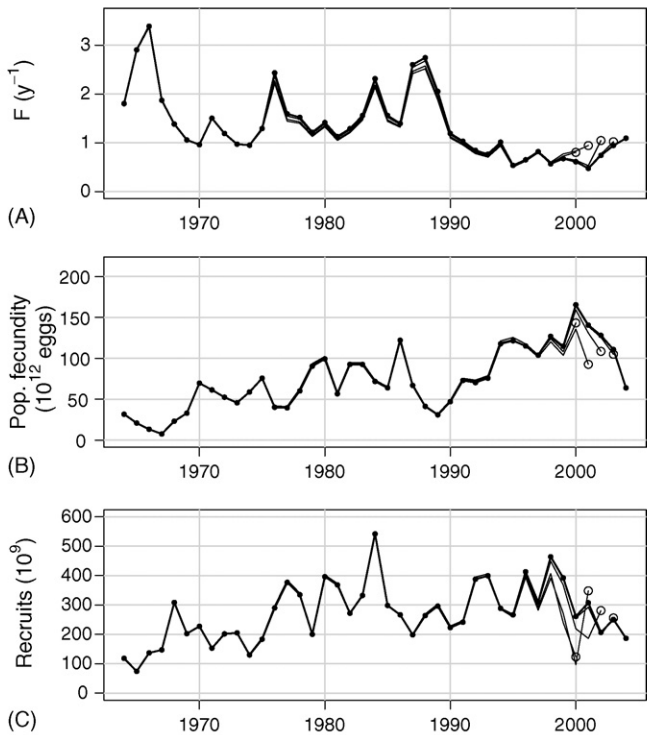

Fig. 7. Estimated time series from the base model (M1; closed circles, bold line) and from models with terminal year 2003 (M7), 2002 (M8), 2001 (M9), and 2000 (M10). Open circles indicate terminal year of models M7–M10. (A) Fully selected fishing mortality rate; (B) population fecundity; and (C) number of age-0 recruits.

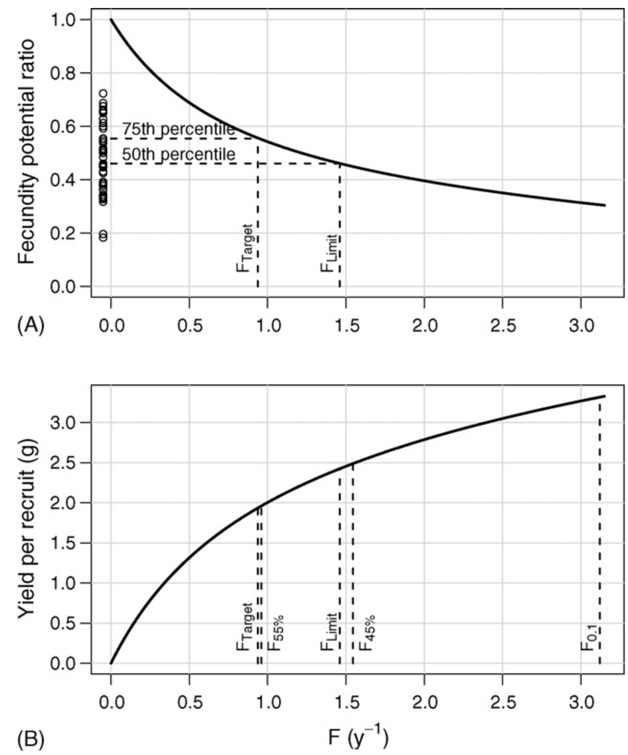

Fig. 8. Per recruit analyses. (A) Fecundity potential ratio based on mean egg production. Circles represent annual estimates of fecundity potential ratio in 1964–2004. From these estimates were computed percentiles and corresponding biological reference points, F_{Target} and F_{Limit}. (B) Yield per recruit, with alternative reference points ($F_{0.1}$, $F_{45\%}$, and $F_{55\%}$) shown for comparison with F_{Target} and F_{Limit}. The yield per recruit curve has no maximum.

was below its target for a healthy stock (Table 6; Fig. 9). Neither terminal-year estimate exceeded its limit.

By assessment standards, terminal-year estimates were relatively precise, with proportional standard error (PSE) of F_{2004} near 0.1, and PSE of Ψ_{2004} near 0.08. Assuming normality and standard errors as estimated, cumulative probability distributions show that each terminal-year estimate is quite likely between its target and limit (Fig. 10).

The alternative reference points estimated for fishing mortality were $F_{0.1} = 3.12$, $F_{45\%} = 1.55$, and $F_{55\%} = 0.96$ (Fig. 8B). The yield per recruit curve did not have a maximum, and thus F_{max} does not exist. For reference to %FRP values, the proposed limit corresponds to $F_{46.1\%}$, and the proposed target to $F_{55.5\%}$ (Fig. 8A).

Fishery status portrayed by sensitivity runs was in general consistent with that of the base model: terminal-year estimates of F and Ψ were between their targets and limits. Two exceptions occurred. Models with high natural mortality or gradual maturity estimated $F_{Terminal}$ to be slightly greater than its limit, and retrospective runs estimated $\Psi_{Terminal}$ to be well above its target.

4. Discussion

The database of gulf menhaden is among the best in the United States. Landings have been monitored comprehensively with rigorous biostatistical sampling since 1964. Additionally, accurate landings data exist back to 1946 because of full disclosure from the industry. Inclusive sampling of the gulf menhaden fishery can be achieved for several reasons: landings dominated by a single user group, cooperative fishing industry, few active ports, and a relatively small number of vessels operated by few companies. Consequently, in addition to being accurate, these data are also precise, at least by fishery standards.

Although precise, the fishery data unavoidably contain some amount of uncertainty. Reduction-fishery landings include mea-

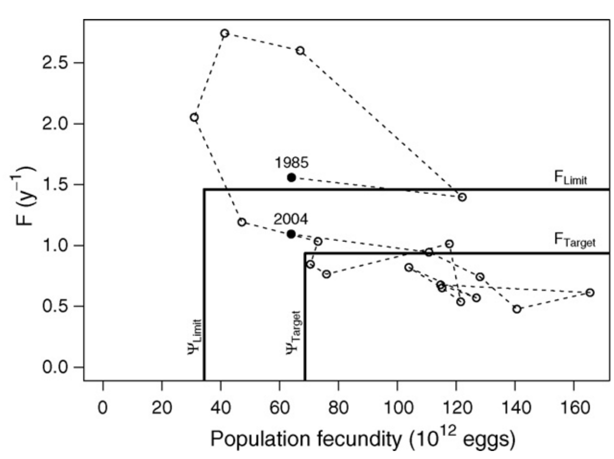

Fig. 9. Target and limit biological reference points (bold lines) from the base model (M1). Overlaid are annual estimates (circles) for 1985–2004, with first and last years indicated (closed circles).

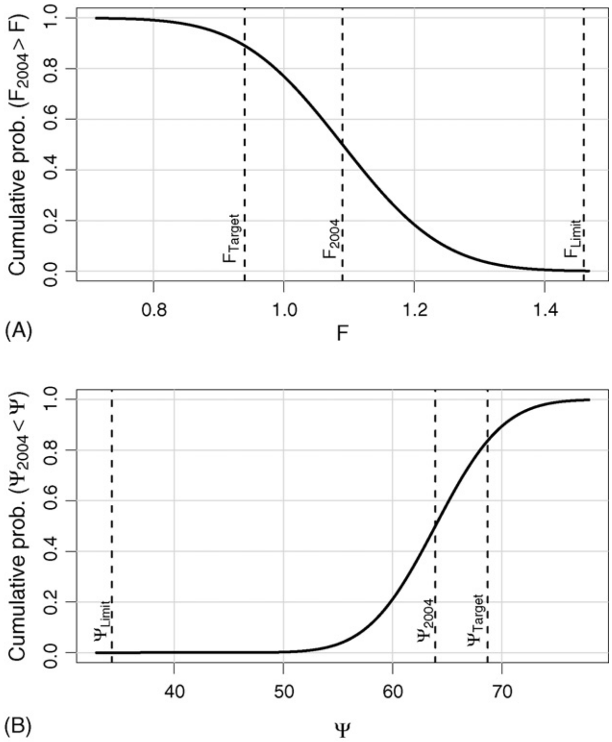

Fig. 10. Precision of 2004 estimates from the base model (M1). (A) Cumulative normal distribution of fully selected fishing mortality rate, centered on $F_{2004} = 0.94$ (0.11 S.E.). (B) Cumulative normal distribution of population fecundity, centered on $\Psi_{2004} = 63.91 \times 10^{12}$ (4.88×10^{12} S.E.). Dashed lines represent 2004 estimates or biological reference points, as indicated.

surement error (CV = 4%) associated with documenting vessel unloads. Bait landings, a minor component of the fishery (generally <1%), are lumped with those of the reduction fishery and assumed to have the same level of uncertainty. Ageing of gulf menhaden is believed to be accurate (Nicholson and Schaaf, 1978). Paired age assignments of recent scale samples ($n = 568$) showed 92% agreement of age-1 fish ($n = 267$) and 80% agreement of age-2 fish ($n = 192$); hence, uncertainty in age composition stems mostly from sampling error, inversely related to effective sample size. Within the two-stage biostatistical sampling design, annual effective sample size (n_t) is the number of 10-fish samples (20-fish samples in 1964–1971) taken during a year, which reflects the belief that all fish of a sample come from the same school and should therefore be treated as a single sampling unit. The large effective sample sizes (Table 1) and high agreement between age assignments imply good precision and accuracy of annual age compositions.

Less precise are the fishery-independent data. The juvenile abundance index included catch-per-unit-effort data collected by several sources, combined according to relative productivity of streams across the northern Gulf of Mexico. Variability in the juvenile abundance index was quantified by bootstrap (CVs range 10–20%), which does not account for propagation of error from sampling or relative productivity of streams, and is therefore likely to overestimate precision.

The assessment model incorporates uncertainty via its likelihood. Thus, fits of the model reflect uncertainties associated with data components. The model fits closely the landings and age composition data, which are sampled with high precision, and less closely the juvenile abundance index.

In the terminal year of data, stock status, as indicated by population fecundity, was estimated to be between its target and limit reference points. This result indicates that the stock is below an ideal level, but not alarmingly so. Likewise, fishing mortality rate in the terminal year was estimated to be between its target and limit, though close to the target. These results should be interpreted in light of retrospective analyses, which suggested that terminal population fecundity may be underestimated and terminal F may be overestimated. With terminal year values near their targets, the gulf menhaden stock appears to be in good condition. However, if recent trends of decreased population fecundity and increased F continue, the stock would approach its limit reference points.

Biological reference points proposed here are based on per-recruit analyses. The estimate of F_{Target} corresponds roughly to $F_{55\%}$, and the estimate of F_{Limit} to $F_{45\%}$. In a theoretical study, these values were found consistent with the fishing rate at maximum sustainable yield (F_{MSY}) for stocks similar to gulf menhaden (Williams and Shertzer, 2003). The value of $F_{0.1} = 3.12$ would correspond to %FPR near 30%. This F seems to us quite risky, as 30% FPR is below the values observed in all but two years (1965 and 1966) of the assessment period 1964–2004.

The proposed F_{Target} is defined as the fishing mortality rate corresponding to the 75th percentile of annual FPR, chosen because of its precedence in management of menhaden (ASMFC, 2004). Its value in this assessment provides a clear buffer between target and limit. In general, the size of that buffer reflects the degree of risk that resource managers are willing to accept, with *risk* defined here as probability of overexploitation. A higher F_{Target} would increase risk, whereas a lower F_{Target} would decrease risk. Either way, the relationship between FPR and F (Fig. 8) could help inform resource managers should they choose a different F_{Target}. Alternatively, a target could be determined with a control rule, such as the Ratio Extended Probability Approach to Setting Targets, or REPAST (Prager et al., 2003). As detailed in Prager et al. (2003), the REPAST control rule is based on probability theory and computes a target from three quantifiable elements: precision of the assessment results, precision of realizing the target, and level of risk considered acceptable by managers.

The proposed F_{Limit} is analogous to F_{rep} (Sissenwine and Shepherd, 1987) and F_{med} (Caddy and Mahon, 1995), but with slight modification to allow for annual variation in fecundity. We assume that our estimate of F_{Limit} leads to replacement on average, justified in part by the long duration of data over which the stock has experienced wide-ranging environmental conditions. This limit reference point based on per-recruit analysis serves as a proxy for F_{MSY} in the presence of a noisy spawner–recruit relationship (Vaughan et al., 2000).

Recruitment of gulf menhaden shows little, if any, relationship with stock size. Any potential relationship appears to be masked by other influences, such as environmental effects. Indeed, Govoni (1997) found a significant, negative correlation between recruitment of gulf menhaden and Mississippi River discharge. That result underscores the value of a comprehensive and precise recruitment index. Such an index would undoubtedly improve the quality of stock assessment, and may even be applied directly to management of this recruitment-driven fishery, by adjusting fishing effort according to recruitment in previous years.

Relative to the recent rise in fishing mortality rate, it is worth noting the severity of the 2005 hurricane season in the northern Gulf of Mexico and its effect on the fishery. In August 2005, Hurricane Katrina struck eastern Louisiana and Mississippi as a strong category three storm, and weeks later, Hurricane Rita made landfall near the Texas–Louisiana border as a category three storm. Of the four menhaden plants, two (Cameron and Empire) closed due to severe damage, and did not reopen until after the start of the 2006 fishing season. The other two plants (Abbeville and Moss Point) reopened in 2005 with limited operation. For the 2005 fishing season, landings declined to their lowest (433,784 t) since 1992 and nominal fishing effort fell to its lowest (322,300 v-t-wks) since 1964 (Table 1). Our point in discussing these events after the terminal assessment year is that we expect F in 2005 and 2006 to fall below the estimated F_{Target}.

Environmental effects may also contribute to the recent rise in fishing mortality rates. Increasingly, extensive areas (up to 20,000 km^2) off the coasts of Louisiana and Texas are marked by low dissolved oxygen in bottom waters, the so-called "dead zone," a combined effect of high summer water temperatures, strong salinity-based water column stratification, periods of reduced mixing, and increased nutrient loads from riverine influx (Rabalais and Turner, 2001). Rather than suffer hypoxia, gulf menhaden probably migrate from areas of low dissolved oxygen, as suggested by the poor or zero catches off central Louisiana when the dead zone impinges close to the shoreline (Smith, 2001). Such displacement is likely to concentrate menhaden schools into narrow coastal corridors making them more susceptible to exploitation, as is suspected of penaeid shrimp (Zimmerman and Nance, 2001). If true, this increased susceptibility, along with decreased recruitment, could account for the recent rise in F.

The rise in F may at first seem puzzling given the coinciding decrease in landings; however, this pattern is consistent with a decrease in abundance (portrayed by population fecundity), which follows declining recruitment. As mentioned previously, fishing effort in 2005 declined because of an active hurricane season, an effect likely to carry over in 2006. Regardless, fishing effort should continue to be monitored and reduced if F approaches its limit.

Acknowledgements

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