Relationship between Gulf Menhaden Recruitment and Mississippi River Flow: Model Development and Potential Application for Management

Author: Vaughan, Douglas S.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 3(1) : 344-352

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2011.620908

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3:344–352, 2011
American Fisheries Society 2011
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2011.620908

ARTICLE

Relationship between Gulf Menhaden Recruitment and Mississippi River Flow: Model Development and Potential Application for Management

Douglas S. Vaughan*[1]
National Marine Fisheries Service, Southeast Fisheries Science Center, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

John J. Govoni
National Oceanic and Atmospheric Administration, National Ocean Service, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

Kyle W. Shertzer
National Marine Fisheries Service, Southeast Fisheries Science Center, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

Abstract
The Gulf menhaden *Brevoortia patronus* is one of the most abundant pelagic fishes in the northern coastal Gulf of Mexico (hereafter, "Gulf") and is the principal forage for various commercial and sport fishes, sea birds, and marine mammals. Part of the life history of Gulf menhaden is spent on the continental shelf and part is spent within estuaries. Adults spawn near the mouth of the Mississippi River, and larvae aggregate within the river plume front. Larval Gulf menhaden transit the continental shelf and enter estuaries of the northern Gulf as juveniles. Govoni (1997) demonstrated an association between the discharge of the Mississippi and Atchafalaya rivers and Gulf menhaden recruitment. In particular, he found an inverse association between Mississippi River discharge and estimated recruitment of half-year-old fish based on recruitment data from Vaughan et al. (1996). Vaughan et al. (2000) updated this relationship with a regression analysis. Here, we revisit the relationship with additional years of data through 2004. The inverse relationship continues to hold. In addition, we reframed this relationship to produce a 1-year-ahead prediction model for forecasting recruitment to age 1 from Mississippi River discharge; this model can be used in proactive fishery management. Finally, we revisited the stock assessment model of Vaughan et al. (2007) and demonstrated an improvement in model performance when information on annual river discharge was incorporated.

The Gulf menhaden *Brevoortia patronus* is an exploited marine resource as well as an integral and key ecological component of the coastal northern Gulf of Mexico (hereafter, "Gulf") ecosystem (Ahrenholz 1981). As both a planktivore and a detritivore, the Gulf menhaden not only provides a key linkage between primary, secondary, and fishery production in the

Subject editor: Donald Noakes, Thompson Rivers University, British Columbia, Canada

*Corresponding author: dvaughan97@gmail.com
[1]Present address: 214 Shell Landing Road, Beaufort, North Carolina 28516, USA.
Received August 4, 2010; accepted March 10, 2011

northern Gulf, it also provides a short circuit for the transfer of detrital energy directly to consumers (Lewis and Peters 1984). The Gulf menhaden is one of the most abundant pelagic fish in the northern coastal Gulf and is the principal forage for various commercial and sport fishes, sea birds, and marine mammals (Ahrenholz 1991). Given these attributes and ecological roles, the Gulf menhaden provides a key indicator of the productivity and health of the ecosystem.

Part of the life history of Gulf menhaden is spent on the continental shelf and part is spent within estuaries (Ahrenholz 1991). Adults spawn primarily near the mouth of the Mississippi River in winter. Larvae aggregate within the river plume front (Govoni et al. 1989), transit the continental shelf, and enter estuaries of the northern Gulf as juveniles. The mechanism of this transit across the extended offshore estuary (Able 2005) is not well understood. Adult Gulf menhaden reoccupy nearshore continental shelf waters, where they feed and reproduce (Ahrenholz 1991).

Recruitment is the process of population dynamics through which individuals must pass before joining adult populations and the habitats they occupy. Gulf menhaden recruitment is correlated with the combined discharge of the Mississippi and Atchafalaya rivers (Govoni 1997). Recruitment of half-year-old Gulf menhaden is inversely correlated with winter and spring discharge rates on an annual scale. When the discharge rate in winter and spring increases from year to year, Gulf menhaden recruitment or year-class strength (as measured by the abundance of half-year-olds) decreases; when discharge decreases, the abundance of half-year-olds increases (Govoni 1997; Vaughan et al. 2000). On an annual scale, this reciprocal association is thought to be related to a mechanism of larval transport. On a decadal scale, there has been an apparently systematic—possibly climate-driven—increase in both river discharge and Gulf menhaden recruitment since the mid-1970s. This association is thought to be related to changes in primary production and consequent secondary production (Govoni 1997) that are driven by nutrients delivered to the northern Gulf by the Mississippi River (Liu and Dagg 2003).

Mississippi River discharge is related to global climate change and the associated hypoxic zone that is evident in the northwestern Gulf (Rabalais et al. 2007; Turner et al. 2008); hypoxia might be another possible correlate of Gulf menhaden recruitment and Mississippi River discharge. Whereas Gulf menhaden spawning and larval growth occur in winter within waters overlying the continental shelf of the northern Gulf (Ahrenholz 1991), the hypoxic zone is a summer phenomenon that is driven ultimately by nutrients delivered to the coastal ecosystem by Mississippi River discharge.

Three objectives were addressed in this study: (1) to test whether the underlying relationship found by Govoni (1997) between recruitment and river discharge continues to hold with more recent recruitment estimates (Vaughan et al. 2007); (2) to recast the statistical relationship in the form of year-ahead forecasts of recruitment to age 1 rather than the recruitment of half-year-olds as was used by Govoni (1997); and (3) to incorporate this relationship into the stock assessment model of Vaughan et al. (2007). The forecasts can be further extended between assessments by using each 1-year prediction as input for additional forecasts. Because Gulf menhaden are short lived (1–4 years; Ahrenholz 1981) and because landings are largely recruitment driven, this approach has the potential to provide real-time management projections of allowable catch.

METHODS

River discharge data and correlation.—Water drained from approximately 40% of the North American continent collects into the Mississippi River (Turner et al. 2008), and flow is diverted downstream into the Mississippi and Atchafalaya rivers. Discharge of the Mississippi and Atchafalaya rivers is controlled and flow is measured by the U.S. Army Corps of Engineers at two locks located north of New Orleans, Louisiana (Figure 1). Discharge data were obtained from the U.S. Army Corps of Engineers (2009a, 2009b) websites for Tarbert Landing, Mississippi (Mississippi River), and for Simmesport, Louisiana (Atchafalaya River). Data are near real time (i.e., available within several days of measurement). Units are daily measurements (provided in ft^3/s [m^3/s]) that are accumulated by month and averaged overwinter (from November through the following March). Flow index data for a given calendar year represent January–March of that year and November–December from the previous calendar year. Our computation of Mississippi River flow indices was identical to the methods described by Govoni (1997). Because river discharge is measured in winter (November–March), data for the most recent year become available in early April (Figure 2).

Vaughan et al. (2007) estimated the recruitment of Gulf menhaden most recently through a statistical catch–age model by using the number of fish in landings at each age (ages 0–6) for each year (1964–2004). Thus, estimates were available for the number of recruits to age 0 in year t (half-year-old fish; $R_{0,t}$) and to age 1 in year $t + 1$ ($R_{1,t+1}$). However, landings of age-0 Gulf menhaden were minor (essentially zero in recent decades), so the relationship between age-0 and age-1 fish within a cohort was mostly a function of natural mortality, which was assumed to vary by age but not by year. Thus, any statistical relationship between age-0 recruits and Mississippi River flow was expected to hold between age-1 recruits (of the same cohort) and Mississippi River flow. In this study, analyses were based on recruits to age 1.

Govoni (1997) compared the change in recruitment to age 0 ($\Delta R_{0,t} = R_{0,t} - R_{0,t-1}$) with the change in river flow ($\Delta F_t = F_t - F_{t-1}$) for the same time period ($t-1, t$). A similar comparison can be made for recruits to age 1 from the same cohort as the age-0 recruits (Figure 3). The year in which fish recruit to age 1 follows the year in which fish from the same cohort recruit to age 0, and hence there is a 1-year lag expressed as

$$R_{1,t+1} = R_{0,t} e^{-Z_{0,t}}, \quad (1)$$

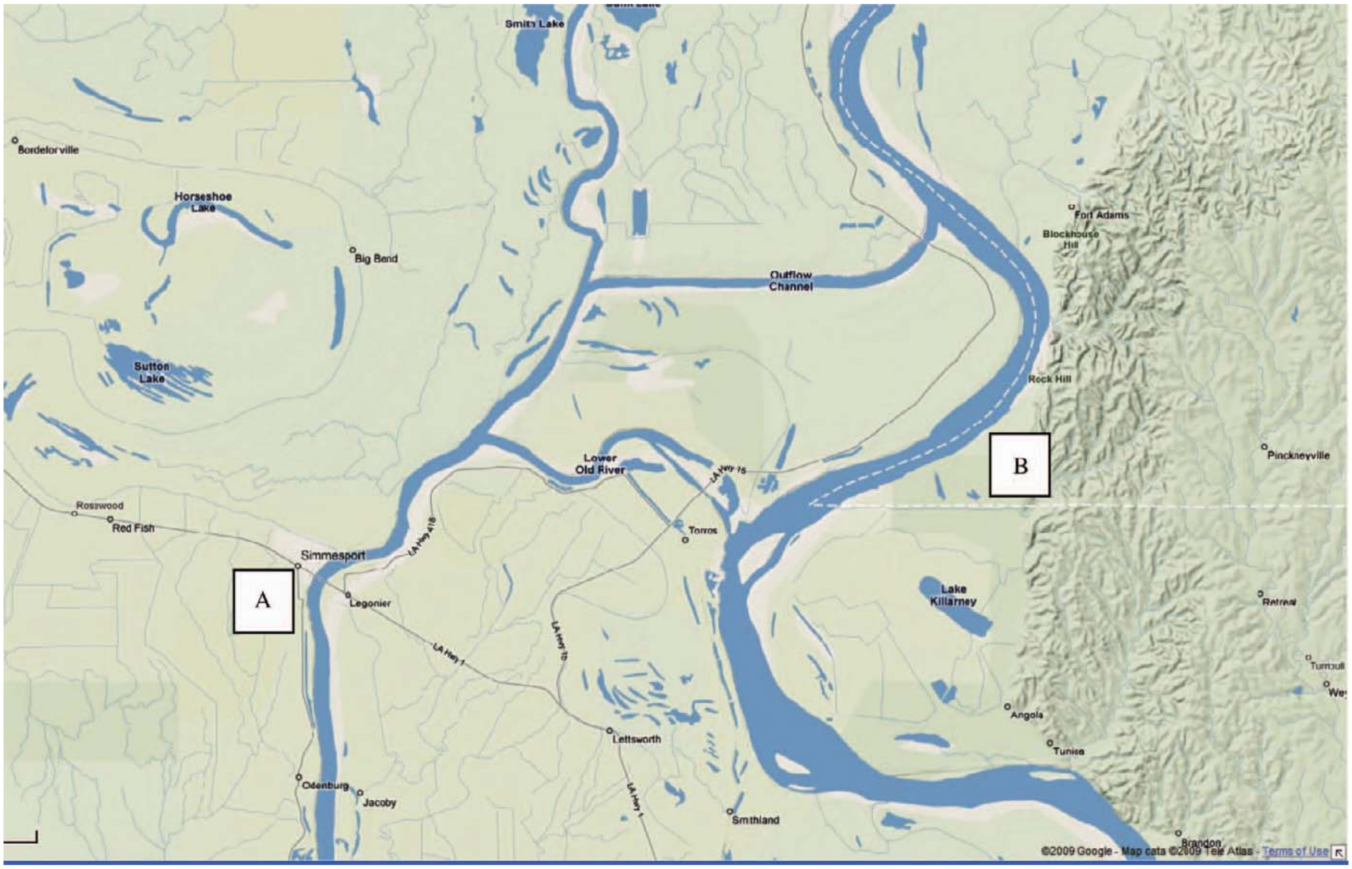

FIGURE 1. Map showing the general locations of U.S. Army Corps of Engineers gaging stations from which discharge data were obtained: **(A)** Atchafalaya River at Simmesport, Louisiana; and **(B)** Mississippi River at Tarbert Landing, Mississippi.

where $Z_{0,t}$ is the instantaneous total mortality rate of age-0 Gulf menhaden, $R_{0,t}$ represents recruits to age 0 in year t, and $R_{1,t+1}$ represents recruits to age 1 in year $t + 1$. With little or no fishing mortality on age-0 fish, $Z_{0,t}$ reduces to M_0, which is the instantaneous natural mortality rate for age 0 and is constant across years.

Regression analyses.—A predictive model was developed by regressing $R_{1,t+1}$ on the 1-year change in river discharge in year t (ΔF_t) and the 1-year lagged recruitment in year t ($R_{1,t}$) with t equal to 1965–2004,

$$R_{1,t+1} = b_0 + b_1 (F_t - F_{t-1}) + b_2 R_{1,t} + \varepsilon, \tag{2}$$

where b_0, b_1, and b_2 are estimated parameters; and error ε is normally distributed $\varepsilon \sim N(0,\sigma^2)$. We used the differenced flow values rather than separate values with their own coefficients for two reasons: (1) to maintain consistency with the methods of Govoni (1997) and (2) more importantly, to address nonstationarity in the river flow data. Determination of nonstationarity was based on autoregressive integrated moving average modeling techniques (Nelson 1973). Equation (2) permits 1-year-ahead forecasting of age-1 Gulf menhaden in the northern Gulf.

Forecasts can be evaluated in two ways. First, a comparison can be made with subsequent estimates of realized (observed) population recruitment from the statistical catch–age model. Alternatively, an evaluation of the historical performance of the regression model can be made by reducing the data set by 1 year (e.g., removing data year 2004 from the 1964–2004 data set), sequentially re-estimating the regression parameters, predicting recruitment for the next year, and comparing that prediction with the observed estimate of recruitment. This retrospective approach was based on equation (2) and was conducted by sequentially reducing the terminal year of recruits to age 1 from 2004 to 1997. This sequential approach allowed us to consider the stability of our regression results as the data were removed.

Projections can be extended beyond 1 year but with increasing uncertainty. By assuming the initial 1-year projection estimate of recruits to age 1 in the terminal year + 1 as "known," we can use that value as the lagged recruits to age 1 in equation (2) to develop an additional projection for the terminal year + 2. This sequence can be computed into the future with available additional years of Mississippi River discharge data. At the time of writing, data through March 2009 were available, so projections of recruits to age 1 were made through 2010.

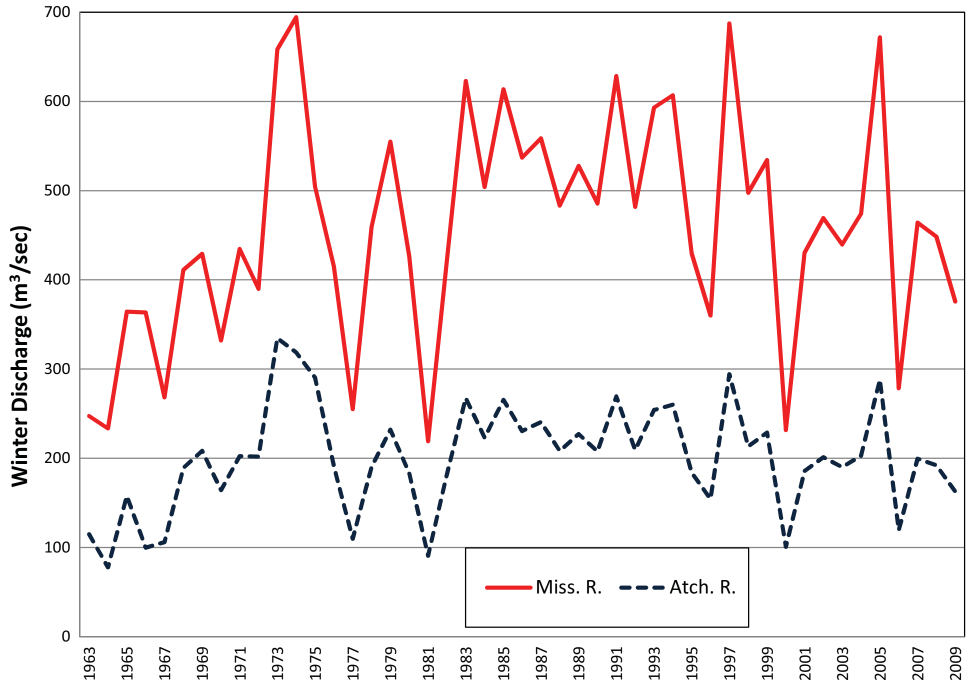

FIGURE 2. Index of mean monthly discharge (m^3/s) for the Mississippi River (Miss. R.) and Atchafalaya River (Atch. R.) during winter (November–March) 1964–2009. Data represent January–March of the given calendar year and November–December from the previous calendar year.

Stock assessment analyses.—To examine the utility of including river discharge in a population model of Gulf menhaden, we applied the stock assessment of Vaughan et al. (2007) but modified the recruitment function to incorporate environmental effects (Schirripa et al. 2009),

$$R^{t+1} = f(S_t|h, R_0)e^{\beta F_{t+1}}, \quad (3)$$

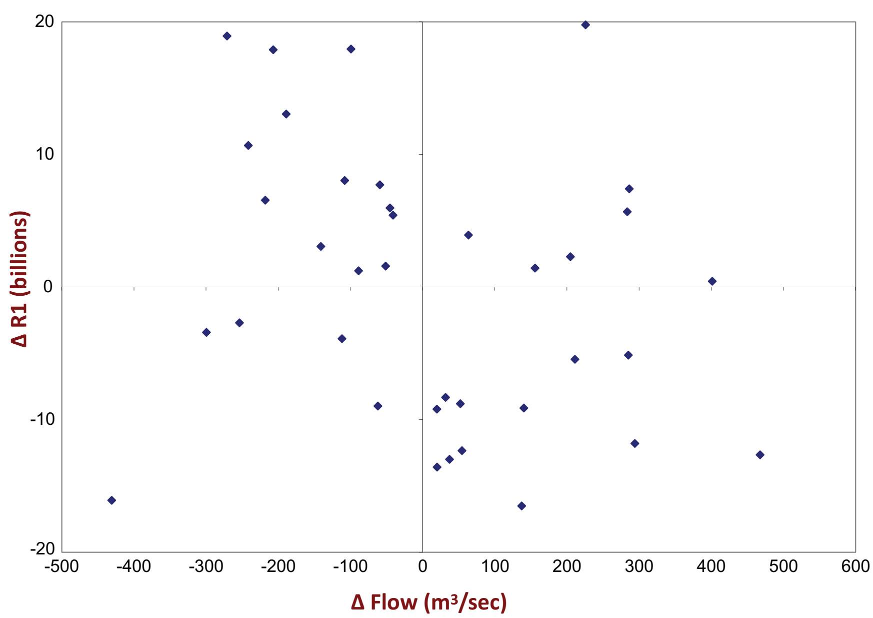

FIGURE 3. Plot of change in Gulf menhaden recruitment to age 1 (ΔR_1) compared with the change in discharge of the Mississippi and Atchafalaya rivers (ΔFlow). Flow and recruits are aligned by cohort year (t – 1, t), so the year of recruitment to age 1 is a year later. The inverse relation between ΔR_1 and ΔFlow is significant ($r^2 = 0.298$; $P < 0.0005$).

TABLE 1. Parameter estimates for models predicting the number of age-1 Gulf menhaden recruits (R_1; equation 2) as function of the change in discharge of the Mississippi and Atchafalaya rivers and 1-year lagged R_1 (note that b_0, b_1, and b_2 were calculated based on river discharge in ft^3/s). Analyses included recruitment estimates from the latest stock assessment (Vaughan et al. 2007) with data through 2004 ($P > F$ is the probability [based on the F-test] that the reduction in sums of squares due to the regression model fit to the data was statistically significant). Robustness of the regression results was illustrated by a retrospective analysis in which recent data were removed and parameter values were re-estimated (see Methods).

Last year of data	n	b_0	b_1	b_2	Adjusted r^2	$P > F$
2004	40	16.22	–0.00044	0.5264	0.298	0.0005
2003	39	16.19	–0.00044	0.5271	0.296	0.0007
2002	38	16.22	–0.00044	0.5338	0.304	0.0007
2001	37	15.84	–0.00048	0.5383	0.316	0.0006
2000	36	14.39	–0.00066	0.5999	0.380	0.0001
1999	35	14.48	–0.00066	0.5957	0.356	0.0003
1998	34	14.86	–0.00056	0.5692	0.325	0.0009
1997	33	15.10	–0.00060	0.5584	0.323	0.0011

where R is predicted recruitment; f is a function of spawners S (here, population fecundity); F is standardized river flow; and h, R_0, and β are parameters (defined in more detail below). Thus, the assessment model here estimated all of the same parameters presented by Vaughan et al. (2007; i.e., annual fishing mortality rates, selectivity parameters, and catchability) except for stochastic annual recruitment deviations. Instead, recruitment was treated as deterministic by using several versions of equation (3) as described below.

We considered two spawner–recruit relationships (i.e., f): Beverton–Holt and Ricker. For each, we applied three variations of equation (3) to examine recruitment as a function of S only, F only, or both S and F. In the first, the β parameter was not estimated but was fixed at zero; thus, equation (3) simplifies to $R_{t+1} = f(S_t|h, R_0)$. In the second variation, h (the steepness parameter) was not estimated but was fixed at a value such that recruitment was independent of S ($h = 1$ for Beverton–Holt; $h = \infty$ for Ricker); thus, equation (3) simplifies to $R_{t+1} = R_0 e^{\beta F_{t+1}}$, where R_0 is interpreted as mean recruitment (rather than the usual interpretation of recruitment that is not harvested). In the third variation, recruitment was a function of both S and F such that equation (3) was applied in full. Thus, the assessment models applied six variations of equation (3) to predict recruitment (however, note that the two variations with fixed h are identical). Using maximum likelihood, the models were fitted to catch–age data and an index of abundance. Computations were conducted with Automatic Differentiation Model Builder software (ADMB Project 2010), and performance was compared among models by use of Akaike's information criterion (AIC).

RESULTS

River Flow Correlation

Correlations comparing the change in Mississippi River discharge with the corresponding change in Gulf menhaden recruitment demonstrated only small differences between the ages of recruitment. The adjusted estimates of r^2 were 0.266 for age-0 recruits and 0.298 for age-1 recruits (Table 1). These relationships therefore explained between 27% and 30% of the variability in the assessment estimates of recruitment.

Regression Analyses

Estimated age-1 recruits generally fit the observed data well; the exception was the estimate for 1985, which fell outside the 95% confidence interval (CI; Figure 4). The width of the 95% CI about the predicted point suggested that a considerable amount of uncertainty remained unexplained (1 – r^2, expressed as a percentage).

Sequentially reducing the terminal year of data resulted in consistent parameter estimates over the final 3–4 years of the data set (terminal years 2001–2004; Table 1). Furthermore, 1-year projection estimates from the sequential regressions compared well with the estimates for the same year based on the regression that included all of the data (Table 2, columns labeled "All data" and "1 year ahead"). These estimates of expected and predicted values indicated good correspondence with stock assessment values in some years but not in others. Only small discrepancies were noted when overlaying the estimates of recruitment among the various retrospective model fits (Figure 5). Estimates of adjusted r^2 ranged from 0.30 to 0.38, depending on the terminal year of the data (Table 1). The magnitude peaked (and the P-value was minimized) when 2000 was used as the terminal year of data. After terminal year 2000, the inclusion of additional data resulted in some deterioration of the regression fit.

One-year projection estimates (and 95% CIs) of recruits to age 1 were compared with the observed values from the stock assessment for projection years 1998–2005 (where projection year = terminal year + 1; Figure 6). The predicted and observed values were close in 2000 and 2004 but were more divergent in other years, especially 2001. In all cases, the observed values fell within the 95% CIs of the predicted values.

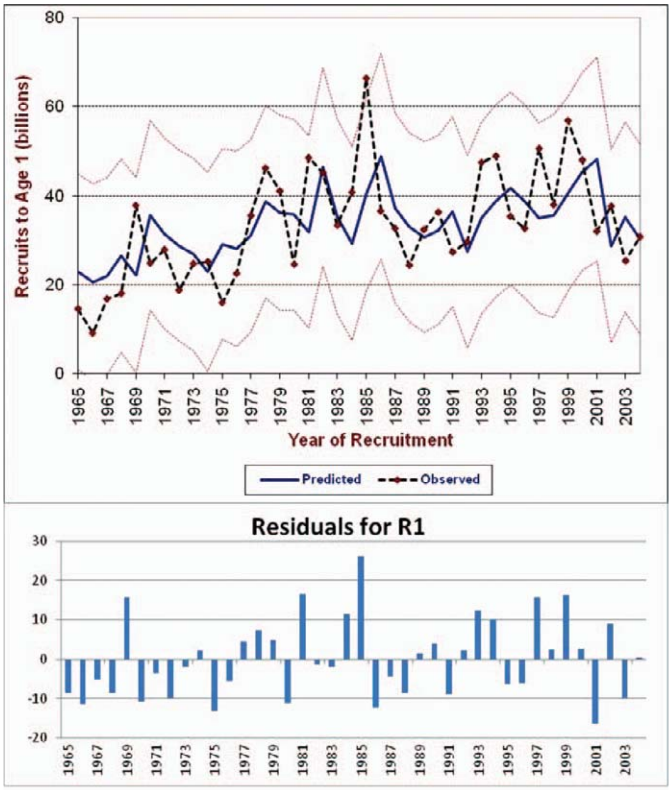

FIGURE 4. Observed estimates of Gulf menhaden recruitment to age 1 (R_1; billions, where 1 billion = 1 × 10^9) and values of R_1 (±95% confidence interval) that were predicted from the 1-year change in discharge (ΔFlow; Mississippi and Atchafalaya rivers) and 1-year lagged R_1 (upper panel); recruitment residuals are also presented (lower panel).

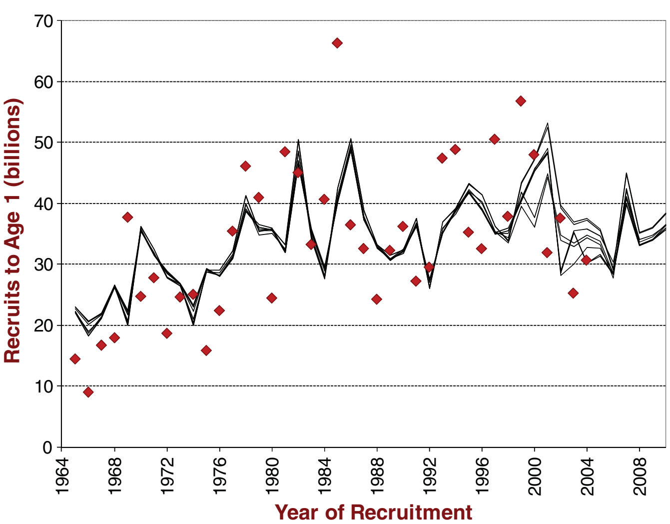

FIGURE 5. Retrospective forecast of Gulf menhaden recruitment to age 1 (R_1; billions, where 1 billion = 1 × 10^9) from the 1-year change in river discharge (ΔFlow; Mississippi and Atchafalaya rivers) and 1-year lagged R_1 (forecast for 1998–2005). Multiyear forecasts through 2010 from each of the retrospective regressions are also shown.

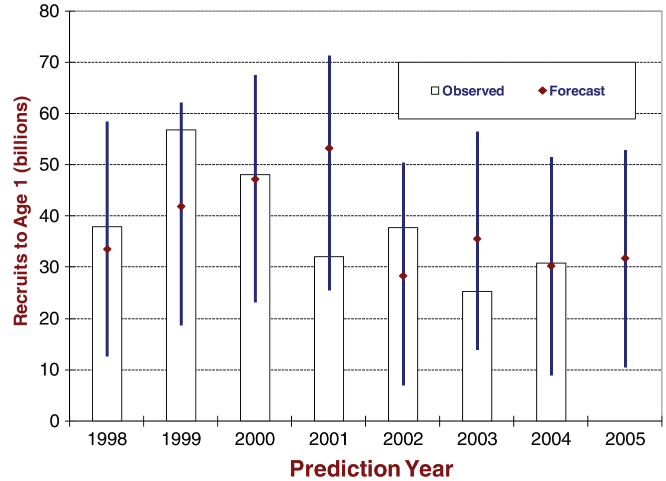

FIGURE 6. Comparison of predicted (±95% confidence interval) and observed values (billions, where 1 billion = 1 × 10^9) of Gulf menhaden recruitment to age 1 by use of re-estimated parameters of equation (2) determined from the reduced data set. Data were available through the terminal year; prediction year is the terminal year + 1.

When all available data through 2004 were assessed, including the terminal year observed value of 30.7 × 10^9 age-1 Gulf menhaden for 2004, the model fit provided an estimate of 30.2 × 10^9 Gulf menhaden for that same year and yielded a 1-year-ahead projection estimate of 31.7 × 10^9 Gulf menhaden for 2005. Extended projections beyond the observed estimates of recruits to age 1 (ending in 2004) were based on available Mississippi River discharge data through 2009 (Figures 4, 5), and the 95% CIs (Figure 4) were inappropriate beyond 2005.

Stock Assessment Analyses

Assessment models that predicted recruitment from spawning stock size performed better than the models that predicted recruitment from river discharge alone (Table 3). The best-performing models were those that predicted recruitment from both spawning stock size and river discharge. This result held true for both the Beverton–Holt and Ricker spawner–recruit functions.

DISCUSSION

Various environmental correlates have been proposed for predicting Gulf menhaden harvests (Stone 1976; Guillory et al. 1983; Guillory 1993). Many of these correlates (e.g., temperature and salinity) are themselves correlated with combined Mississippi River discharge. Because Gulf menhaden landings depend primarily on ages 1–3 (age 2 typically dominates the landings; Vaughan et al. 2007), the Gulf menhaden fishery is largely recruitment driven. Therefore, an understanding of Gulf menhaden recruitment dynamics is important for proactive management.

With the addition of new data, the relationship first observed by Govoni (1997) still holds. In contrast, established

TABLE 2. Observed (estimated) Gulf menhaden recruitment to age 1 (R_1; × 10^9) and values of R_1 that were predicted from all data and by use of 1-year-ahead projection from retrospective runs. The 95% confidence limits (CLs) are based on the retrospective regressions with reduced data.

		Predicted R_1 for terminal year + 1		95% CL	
Projection year	Observed R_1	All data	1 year ahead	Lower	Upper
1998	37.9	35.5	33.5	12.7	58.4
1999	56.9	40.4	41.8	18.6	62.2
2000	48.1	45.3	47.1	23.2	67.5
2001	32.0	48.3	53.2	25.4	71.2
2002	37.7	28.6	28.2	6.9	50.3
2003	25.3	35.2	35.5	13.9	56.5
2004	30.7	30.2	30.2	8.8	51.5
2005		31.7	31.7	10.4	52.9

correlations between environmental variables and recruitment are often found to degrade over time. For example, an initial relationship between recruitment of Atlantic menhaden *B. tyrannus* and Ekman transport (Nelson et al. 1977) was later found to no longer hold with the addition of more years of data. This is partly attributable to the large influence of the 1958 year-class on the original relationship and to the lack of veracity of Ekman transport as a causative agent in Atlantic menhaden recruitment. The addition of more years of data diluted the original results. More recently, McClatchie et al. (2010) reassessed the temperature–recruit relationship for the Pacific sardine *Sardinops sagax* and found that this relationship no longer held; thus, those authors recommended that the relationship be removed from Pacific sardine management.

Uncertainty associated with model fits assumes that the independent variables (Mississippi River discharge and the previous year's recruits to age 1) are known without error. Because this is not strictly true, the 95% CIs presented here should be considered underestimates of true uncertainty. Although the observed value falls within the 95% CI about the predicted point, the width of these CIs suggests the need to explore additional environmental factors that might expand the current model framework to further reduce uncertainty and improve the predictive power of the model.

Gulf menhaden assessments have been conducted on an approximately 5–7-year cycle, beginning with Ahrenholz (1981), followed by Vaughan (1987) and then by Vaughan et al. (1996, 2000, 2007). Between assessments, a priori knowledge of recruits to age 1 should help the fishing industry adjust their effort and should assist the Gulf States Marine Fisheries Commission in making their regulatory recommendations. Thus, to the extent that the Mississippi River discharge is informative of the recruitment process for Gulf menhaden, this relationship can benefit the management process. In particular, it may help in cases when unusually weak or strong recruitment events are predicted.

To bridge the gap since the terminal year (2004) of the last assessment (Vaughan 2007), we attempted to provide estimates of Gulf menhaden recruitment through 2010 (Figures 4, 5) by using Mississippi River discharge data through winter 2008. These extended 1-year-ahead forecasts used the previous year's prediction as the basis for the next year. Although such forecasts can

TABLE 3. Comparison of assessment models with different functions for predicting recruitment of Gulf menhaden. The models applied either the Beverton–Holt (BH) or Ricker (R) spawner–recruit (SR) relationship. The steepness parameter (h) was either estimated (Y) or not estimated (N); if not estimated, h was set to a value where recruitment was independent of spawning size, such that the remaining parameter of the SR relationship described mean recruitment (thus, models 2 and 5 are the same). Similarly, the β parameter, which describes the effect of standardized river discharge on recruitment, was either estimated (Y) or fixed at zero (N). Also presented are the number of parameters in the full assessment model, the negative log likelihood ($-\log[L]$) of the fit to the data, and Akaike's information criterion (AIC; lower AIC indicates better model performance).

Model	SR	h estimated?	β estimated?	Number of parameters	$-\log(L)$	AIC
1	BH	Y	N	50	1,728.5	3,557.0
2	BH	N	Y	50	2,013.2	4,126.4
3	BH	Y	Y	51	1,555.3	3,212.6
4	R	Y	N	50	1,705.3	3,510.6
5	R	N	Y	50	2,013.2	4,126.4
6	R	Y	Y	51	1,541.6	3,185.2

provide useful information, we note that the iterative approach leads to increasing uncertainty in subsequent forecasts.

Over the years, significant improvements in available information have resulted in a broader array of modeling approaches for use with stock assessments. For example, earlier assessments assumed that natural mortality was constant across ages and that the catch–age matrix was known without error. In addition, these assessments did not directly incorporate state-specific, fishery-independent indices of recruitment (Vaughan 1987; Vaughan et al. 1996, 2000). The most recent assessment incorporated these new data with less-restrictive assumptions (Vaughan et al. 2007).

Our results suggest that future assessments could be improved further by including river discharge as an environmental covariate for the modeling of recruitment. Whether Beverton–Holt or Ricker functions were used, the inclusion of river flow information enhanced model performance as indicated by AIC (Table 3). Furthermore, the AIC indicated that the Ricker function outperformed the Beverton–Holt function; however, we caution against the use of AIC values to select between them. The two functions can lead to quite different management advice, and we agree with previous authors (Williams and Shertzer 2003) that the Ricker function should be used only with convincing evidence that its underlying mechanisms are in play. In either case, the inclusion of environmental covariates could be accomplished by modifying the spawner–recruit function (as we have done here) or by using the time series of environmental data as an index with which to tune annual recruitment deviations (Schirripa et al. 2009).

Although our focus was on recruitment, various statistical approaches have also been used to forecast harvests of Atlantic menhaden and Gulf menhaden (Schaaf et al. 1975; Hanson et al. 2006). In particular, several forecasting techniques were compared in a setting analogous to that in our study (Hanson et al. 2006), including the multiple regression approach used here, multivariate time series (e.g., state space modeling), and artificial neural networks. The multiple regression approach performed as well as or better than the alternative approaches.

Mississippi River discharge may have an indirect influence on the northern Gulf ecosystem and on fisheries recruitment. Since the 1940s, nutrient loads discharged by the river have increased owing to changes in agricultural practices on the North American continent (Turner et al. 2008). The increased nutrient loads have resulted in a zone of hypoxic water in the northern Gulf region west of the Mississippi Delta. The apparent sensitivity of adult Gulf menhaden to hypoxic conditions was evident in summer 1995, when exceptionally low catches off the Louisiana coast from Southwest Pass westward to Marsh Island co-occurred with the impingement of hypoxic waters upon Louisiana's nearshore waters (Smith 2000). Hypoxic water is near the bottom; consequently, the sensitivity of Gulf menhaden juveniles is probably related to the interaction of habitat displacement and the shoreward, deepwater movement of these fish (Craig and Crowder 2005). Persons responsible for assessing the impact and consequences of hypoxia in the northern Gulf, along with those responsible for appraising the impact of global climate change, should benefit from the forecast of Gulf menhaden, a key ecological species that responds to annual changes in runoff and Mississippi River discharge.

Environmental changes influence ecosystems (Kimmel et al. 2009). Mississippi River discharge, which is determined by precipitation and runoff, varies on decadal and annual scales. Mississippi River and Atchafalaya River discharge rose from 1963 to a peak in 1974, declined, and became erratic from 1976 to 2009, especially over the last decade (Figure 2). Although Gulf menhaden recruitment has been relatively variable from year to year, recruits to age 0 generally rose from 1963 to a peak in 1984, declined, and then gradually rose to a more recent peak in 1998, which was followed by an overall decline. Recruits to age 1 show the same pattern but with a 1-year lag (Figure 4). Thus, both river discharge and recruitment demonstrate significant annual variability and, as suggested by the regression model, they do so in an inverse fashion. Long-term patterns in these two variables are not as well linked. Annual- and decadal-scale change in the relationship between Gulf menhaden abundance and river discharge may well signal an ecosystem regime shift (sensu Steele 1998) in the northern Gulf ecosystem.

Models are essential for forecasting the effects of ecosystem change on fisheries recruitment and consequent production. The influence of temperature, salinity, and river discharge on fish recruitment has been well documented (Drinkwater and Frank 1994; Grimes and Kingsford 1996; Gillanders and Kingsford 2002), but few comprehensive predictive models are available. Within estuaries, river discharge is correlated with growth and survival of young fish (North and Houde 2003; Shoji and Tanaka 2006). A threshold for the influence of salinity and flow rate on the abundance of young fish (including other estuarine-dependent, herringlike fish) is evident wherein a positive relationship becomes negative (Strydom et al. 2002; Whitfield and Harrison 2003). Mississippi River discharge influences fishery production in the northern Gulf, but its direct influence on the recruitment of other stocks may be either positive or negative (Grimes 2001).

The models presented here are directly applicable to forecasting the effects of Mississippi River discharge on Gulf menhaden production and can be used in fisheries and ecosystem management. We have demonstrated that the association reported by Govoni (1997) continues to hold with the analysis of additional, more recent data. We have developed a regression methodology for near-term forecasts that can allow management organizations to make the better-informed decisions that are required to proactively manage Gulf menhaden. Finally, we have demonstrated that the inclusion of river flow improves the performance of the most recent Gulf menhaden stock assessment model (Vaughan et al. 2007).

ACKNOWLEDGMENTS

We thank J. W. Smith, M. Cieri, and one anonymous reviewer for providing valuable reviews of this manuscript. Views expressed are those of the authors and do not necessarily represent the findings or policy of any government agency. Reference to trade names does not imply endorsement by the U.S. Government.

REFERENCES

Able, K. W. 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuarine Coastal and Shelf Science 64:5–17.

ADMB Project (Automatic Differentiation Model Builder Project) 2010. AD Model Builder: Automatic Differentiation Model Builder. Available: www.admb-project.org. (July 2010).

Ahrenholz, D. W. 1981. Recruitment and exploitation of Gulf menhaden, *Brevoortia patronus*. U.S. National Marine Fisheries Service Fishery Bulletin 79:325–335.

Ahrenholz, D. W. 1991. Population biology and life history of the North American menhaden, *Brevoortia* spp. U.S. National Marine Fisheries Service Marine Fisheries Review 53(4):3–19.

Craig, J. K., and L. B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. Marine Ecology Progress Series 294:79–94.

Drinkwater, K. F., and K. T. Frank. 1994. Effects of river regulation and diversion on marine fish and invertebrates. Aquatic Conservation: Freshwater and Marine Ecosystems 4:135–151.

Gillanders, B. M., and M. J. Kingsford. 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. Oceanography and Marine Biology an Annual Review 40:233–309.

Govoni, J. J. 1997. The association of the population recruitment of Gulf menhaden, *Brevoortia patronus*, with Mississippi River discharge. Journal of Marine Systems 12:101–108.

Govoni, J. J., D. E. Hoss, and D. R Colby. 1989. The spatial distribution of larval fishes about the Mississippi River plume. Limnology and Oceanography 34:178–187.

Grimes, C. B. 2001. Fishery production and the Mississippi River discharge. Fisheries 26(8):17–26.

Grimes, C. B., and M. J. Kingsford. 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? Marine and Freshwater Research 47:191–208.

Guillory, V. 1993. Predictive models for Louisiana Gulf menhaden harvests: an update. Louisiana Department of Wildlife and Fisheries, Technical Bulletin 43, Bourg.

Guillory, V., J. Geaghan, and J. Roussel. 1983. Influence of environmental factors on Gulf menhaden recruitment. Louisiana Department of Wildlife and Fisheries, Technical Bulletin 37, New Orleans.

Hanson, P. J., D. S. Vaughan, and S. Narayan. 2006. Forecasting annual harvest of Atlantic and Gulf menhaden. North American Journal of Fisheries Management 26:753–764.

Kimmel, D. G., W. D. Miller, L. W. Harding, E. D. Houde, and M. R. Roman. 2009. Estuarine ecosystem response captured using a synoptic climatology. Estuaries and Coasts 32:403–409.

Lewis, V. P., and D. S. Peters. 1984. Menhaden – a single step from vascular plant to fishery harvest. Journal of Experimental Marine Biology and Ecology 84:95–100.

Liu, H., and M. Dagg. 2003. Interactions between nutrients, phytoplankton, growth, and micro- and mesozooplankton grazing in the plume of the Mississippi River. Marine Ecology Progress Series 258:31–42.

McClatchie, S., R. Goericke, G. Auad, and K. Hill. 2010. Re-assessment of the stock-recruit and temperature-recruit relationships for Pacific sardine. Canadian Journal of Fisheries and Aquatic Sciences 67:1782–1790.

Nelson, C. R. 1973. Applied time series analysis for managerial forecasting. Holden-Day, San Francisco.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Fishery Bulletin 75:23–41.

North, E. W., and E. D. Houde. 2003. Linking ETM physics, zooplankton prey, and fish early-life histories to striped bass *Morone saxatilis* and white perch *M. americanus* recruitment. Marine Ecology Progress Series 260:219–236.

Rabalais, N. N., R. E. Turner, B. K. Sen Gupta, D. F. Boesch, P. Chapman, and M. C. Murrell. 2007. Characterization and long-term trends of hypoxia in the northern Gulf of Mexico: does the science support the action plan? Estuaries and Coasts 30:753–772.

Schaaf, W. E., J. E. Sykes, and R. B. Chapoton. 1975. Forecasts of Atlantic and Gulf menhaden catches based on the historical relation of catch and fishing effort. U.S. National Marine Fisheries Service Marine Fisheries Review 37(10):5–9.

Schirripa, M. J., C. P. Goodyear, and R. M. Methot. 2009. Testing different methods of incorporating climate data into the assessment of US West Coast sablefish. ICES Journal of Marine Science 66:1605–1613.

Shoji, J., and M. Tanaka. 2006. Influence of spring river flow on the recruitment of Japanese seaperch *Lateolabrax japonicas* into the Chikugo estuary, Japan. Scientia Marina 70:159–164.

Smith, J. W. 2000. Distribution of catch in the gulf menhaden, *Brevoortia patronus*, purse seine fishery in the Northern Gulf of Mexico from logbook information: are there relationships to the hypoxic zone? Pages 311–320 *in* N. N. Rabelais and R. E. Turner, editors. Coastal hypoxia: consequences for living resources and ecosystems. Coastal and estuarine studies. American Geophysical Union, Symposium 58, Washington, D.C.

Steele, J. H. 1998. Regime shifts in marine ecosystems. Ecological Applications 8:33–36.

Stone, J. H. 1976. Environmental factors relating to Louisiana menhaden harvest. Louisiana State University, Center for Wetland Resources, Sea Grant Publication, LSU-T-76-004, Baton Rouge.

Strydom, N. A., A. K. Whitfield, and A. W. Paterson. 2002. Influence of altered freshwater flow regimes on abundance of larval and juvenile *Gilchristella aestuaria* (Pisces: Clupeidae) in the upper reaches of two South African estuaries. Marine and Freshwater Research 53:431–438.

Turner, R. E., N. N. Rabalais, and D. Justic. 2008. Gulf of Mexico hypoxia: alternate states and a legacy. Environmental Science and Technology 42:2323–2327.

U.S. Army Corps of Engineers. 2009a. Discharge data Mississippi River at Tarbert Landing, Mississippi. Available: www.mvn.usace.army.mil/cgi-bin/wcmanual.pl?01100. (April 2009).

U.S. Army Corps of Engineers. 2009b. Stage and discharge data Atchafalaya River at Simmesport, Louisiana. Available: www.mvn.usace.army.mil/cgi-bin/watercontrol.pl?03045. (April 2009).

Vaughan, D. S. 1987. Stock assessment of the Gulf menhaden, *Brevoortia patronus*, fishery. NOAA Technical Report NMFS 58.

Vaughan, D. S., J. W. Smith, and E. J. Levi. 1996. Population characteristics of Gulf menhaden, *Brevoortia patronus*. NOAA Technical Report NMFS 125.

Vaughan, D. S., J. W. Smith, and M. H. Prager. 2000. Population characteristics of Gulf menhaden, *Brevoortia patronus*. NOAA Technical Report NMFS 149.

Vaughan, D. S., K. W. Shertzer, and J. W. Smith. 2007. Gulf menhaden (*Brevoortia patronus*) in the U.S. Gulf of Mexico: fishery characteristics and biological reference points for management. Fisheries Research 83:263–275.

Whitfield, A. K., and T. D. Harrison. 2003. River flow and fish abundance in a South African estuary. Journal of Fish Biology 62:1467–1472.

Williams, E. H., and K. W. Shertzer. 2003. Implications of life-history invariants for biological reference points used in fishery management. Canadian Journal of Fisheries and Aquatic Sciences 60:710–720.