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Carolyn N. Belcher and Cecil A. Jennings

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Evaluation of Stock–Recruitment Curves for White Shrimp in Georgia

CAROLYN N. BELCHER*

Commercial Fisheries Research Program, University of Georgia Marine Extension Service, 715 Bay Street, Brunswick, Georgia 31520, USA

CECIL A. JENNINGS

U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, D. B. Warnell School of Forest Resources, University of Georgia, Athens, Georgia 30602, USA

Abstract.—Georgia's food shrimp fishery is currently managed on the premise that a relationship exists between the abundance of spring-spawning white shrimp *Litopenaeus setiferus* and the abundance of fall recruits. Spawners are caught primarily during May and June, and fall recruits are caught from August through January. The efficacy of this management approach is unknown because the relationship between the two segments of the shrimp fishery has never been evaluated. We applied Beverton–Holt and Ricker spawner–recruit curves to fishery-independent and fishery-dependent indices to determine whether spawner abundance could be used to reliably predict the abundance of fall recruits. The commercial landings (lb) from May and June combined were used as the fishery-dependent spawner index, and monthly catch-per-unit-effort (CPUE) values observed during April, May, and June were used as fishery-independent spawner indices. Potential spawner–recruit models were evaluated for each set of indices and the resulting mean square error (MSE) values were compared. The best-fitting model was a Beverton–Holt curve that incorporated June CPUE as the spawner index. Unfortunately, this model was not very predictive. Multiple-regression techniques also were used to select environmental variables that enhanced the fit of the spawner–recruit model. Three two-variable models were evaluated for predictive fit, and the best model (r^2 = 0.447) included September salinity and October water temperature. Our results suggest that the abundance of white shrimp spawners is a poor predictor of the abundance of fall recruits. Inclusion of environmental factors, such as seasonal salinity and water temperature, can improve our ability to predict recruit abundance.

The white shrimp *Litopenaeus setiferus* is a short-lived (i.e., 1 year) species that has high commercial importance throughout much of the South Atlantic Bight (SAFMC 1981). The white shrimp spawning season extends from May through September, but the height of the spawning season occurs during late spring and early summer in shallow waters off coastal beaches. Larval and nauplian development occurs mostly in sounds and estuaries (SAFMC 1981; Shipman et al. 1981). As white shrimp reach maturity, individuals migrate from estuaries and sounds to the nearshore waters, where they recruit into the fall fishery (SAFMC 1981). Although limited migrations occur along the coastline (e.g., northward and southward), most of the shrimp landed by the commercial fleet are caught within 25 nautical miles of the rearing estuary (Shipman et al. 1981). As a result, individual state management plans are more effective than regional plans in managing local landings.

Georgia's food shrimp industry is the most economically important commercial fishery in the state and ranks second behind the hard-shell blue crab *Callinectes sapidus* fishery in terms of total weight (Califf 2000). White shrimp account for about 80% of the commercial shrimp harvested in Georgia, with annual landings averaging about 3.7 million pounds (Roberson 2000). The bulk of commercial white shrimp landings is caught by the fall fishery, which occurs from August to January in Georgia's nearshore waters (within 3 mi of the coast); however, substantial quantities also are caught during May and June in both nearshore and offshore waters (outside of 3 mi).

Georgia's commercial shrimp fishery is divided into two distinct components: commercial food shrimping and sport-bait shrimping. The largest component is the commercial food shrimp fishery, which is primarily a trawl fishery. The Georgia Department of Natural Resources (GADNR) reg-

* Corresponding author: cbelcher@uga.edu

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ulates this fishery under seasonal, area, and gear constraints. Historically, the opening day of the commercial food shrimp season in Georgia occurred during mid- to late June to protect the spawning stock of white shrimp. Generally, the South Carolina white shrimp fishery opened before the Georgia fishery. As a result, many Georgia trawlers went to South Carolina to fish, thus increasing the amount of localized fishing pressure. Likewise, when the commercial season opened in Georgia, the South Carolina trawlers fished in Georgia. Concerns expressed by the industry regarding the staggering of opening days between South Carolina and Georgia and its effect on the spawning stock led to a change in the tentative opening date from June 1 to May 15, starting in 1998. The simultaneous opening of the seasons in the two states provided a larger fishing area to the fleet, which was believed to minimize fishing pressure on the spawning stock.

Currently, Georgia waters are open to commercial food shrimping between May 15 and December 31, provided that shrimp are of sufficient size and quantity. The commercial season can be extended through the end of February if shrimp size and quantity continue to be sufficient. Mechanically retrieved nets are limited to fishing on the seaward side of the sounds; however, the sounds are sometimes open to commercial trawling. Partial open seasons were implemented in the sounds during 1983, 1985, 1986, 1988, and 1989, but the general practice since 1976 has been full-time closure. Cast nets (other than bait-shrimp cast nets) and seines were only recently included in the regulation of the commercial food shrimp fishery; these gear types can be used in the marine waters of Georgia anytime during the open food shrimp season.

Sport-bait shrimping, the second component of the commercial shrimp fishery, operates under area restrictions rather than a defined season. Bait shrimping management zones generally are located in smaller rivers and creeks and are determined by the commissioner of GADNR or his designee. In the event of a disaster or emergency situation, the GADNR can close any or all of the marine waters of the state to both commercial and recreational fishing.

Commercial shrimpers in Georgia believe, as does the GADNR, that white shrimp spawner protection during spring helps to produce a successful fall harvest. As a result, the GADNR manages the Georgia shrimp fishery to protect potential spawners during the spring. Further, the GADNR uses fishery-independent assessments of spawner abundance during spring to determine the opening date of the shrimping season. This approach is based on the premise that a higher abundance of spawners during the spring will result in a higher abundance of harvestable adults during the fall. This relationship is believed to follow density-dependant regulation of shrimp populations (i.e., Beverton–Holt spawner–recruit curves; Jim Music, GADNR, personal communication). The net result of this approach is that higher spring spawner abundances translate to earlier season openings compared to years in which spring abundance is low. It is unknown whether the assumptions underlying the approach are valid, because specific tests of these models have not been previously undertaken.

Spawner–recruit models have been developed for white shrimp stocks in South Carolina (Lam et al. 1989) and in the southwestern Gulf of Mexico (Gracia 1991). Lam et al. (1989) developed a model based on a Beverton–Holt relationship, whereas Gracia (1991) structured his model around a Ricker relationship. Both authors developed models in which the indices for spawners and recruits were represented in the same units. Lam et al. (1989) used commercial landings in kilograms; Gracia (1991) used numbers of individuals. Because of conflicting opinions regarding the underlying spawner–recruit relationship for white shrimp, both the Beverton–Holt and Ricker models should be used in any assessment of the fishery-dependent and fishery-independent data.

Some authors (e.g., Ricker 1975; Lam et al. 1989) have incorporated environmental variables into their models as a means of decreasing the amount of uncertainty surrounding spawner–recruit relationships. For example, salinity and water temperature have been correlated with abundance of several penaeid species (see review in Lam et al. [1989]). Most of the studies reviewed by Lam et al. (1989) used indirect environmental measures, such as number of heating degree-days, rainfall, river discharge, water level, and ocean currents; however, some used direct measures of salinity and water temperature.

In this paper, we evaluate the de facto models that the GADNR uses to manage the Georgia white shrimp fishery. Our objectives were to determine (1) whether a relationship exists between white shrimp spawner abundance during the spring and the abundance of fall recruits and (2) whether environmental factors, such as water temperature and salinity, are useful predictors of the abundance of fall recruits.

Methods

Fishery-dependent variables.—The data used to evaluate spawner–recruit models were collected and maintained by the GADNR Commercial Fisheries Program. The GADNR Cooperative Statistics Program collects data on monthly landings for all commercial fisheries, along with additional fishery-dependent data (e.g., area fished, effort, gear types, and market grades/values) (Califf 2000). Creel agents collect landings data from known dealers in each of the six coastal Georgia counties (Chatham, Bryan, Liberty, McIntosh, Glynn, and Camden). Although commercial landings data have been collected since 1956, fishery-independent surveys have only been conducted since 1968. We developed models with data from 1979 to 2000 because of the consistency of sampling methods employed during that period. However, two of the years (1980 and 1982) were omitted from the time series because data from specific months of interest were missing.

To evaluate both the Beverton–Holt and Ricker models, we used fishery-dependent data as indices for spawners and recruits. The total pounds of white shrimp caught during May–June represented spawners, whereas the total pounds of white shrimp caught during August–January represented recruits. Although Georgia's commercial shrimp season can continue into February, only two years in the series showed substantial landings during that month; therefore, February landings were not included in the fishery-dependent recruit index.

Fishery-independent variables.—The fishery-independent data used for spawner indices were collected from the GADNR research vessel *Anna* during monthly assessment cruises that sampled relative abundance, distribution, size, reproductive stages, and recruitment of penaeid shrimp (Roberson 2000). Sampling was conducted coastwide at 36 fixed stations (Figure 1) in the six commercially important sound systems (Wassaw, Ossabaw, Sapelo, St. Simons, St. Andrew, and Cumberland). Sample stations were distributed among the three general types of staging area for shrimp (large creeks/rivers, sounds, and nearshore/offshore).

Sampling was conducted with a 12.2-m flat net composed of 4.8-cm stretched-mesh webbing in the body and bag. Samples were generally collected during the first half of each month, and on neap tides when possible. Fifteen-minute tows were made at each station; tow speeds were maintained at 2.0 knots when towing against the tide or at 2.5 knots when towing with the tide. Salinity (ppt) and water temperature (°C) were measured during each tow. Salinity at the surface was measured with either a hand-held refractometer or a Yellow Springs Instruments, Inc., (YSI) model 85. Surface temperature was measured with either a standard mercury thermometer or a YSI model 85.

Catches from each tow were sorted by shrimp species, and total weights for each species were recorded. Samples of 30 individuals from each species were measured for total length (tip of rostrum to tip of telson; mm), and information regarding sex, reproductive development, and incidence of disease were recorded (Roberson 2000).

Catch per unit effort (CPUE) values for May and June were used as fishery-independent spawner indices. May and June are the months with the highest percentages (collectively greater than 80%) of white shrimp exhibiting gonadal development (Roberson 2000). However, because spawning can occur early (e.g., April) during some years, the relationship between April CPUE and fall recruit abundance was also evaluated. Significant Pearson's correlations ($P < 0.05$) among the three months suggested that these fishery-independent indices could function as adequate measures of abundance of the spawning stock.

Model development.—The Beverton–Holt equation (Ricker 1975),

$$R = \frac{S}{\alpha S + \beta}, \tag{1}$$

and the Ricker equation (Ricker 1975),

$$R = \alpha S e^{-\beta S}, \tag{2}$$

where R is the recruitment index, S is the spawner index, and α and β are parameters of the relationship, were fit to the spawner and recruit indices by use of methods discussed by Ricker (1975) and ASMFC (2000). We used Microsoft Excel and its Solver add-in to fit the equations based on minimization of the error sum of squares (SSE).

Environmental factors may adversely affect the fit for many of the developed spawner–recruit relationships (Gracia 1991). Therefore, two different techniques commonly used for variable selection in multiple regression (Ricker 1975; Lam et al. 1989) were applied to monthly water temperature and salinity values collected during May–December. The majority of shrimp recruitment occurs in August–October; therefore, the effects of environ-

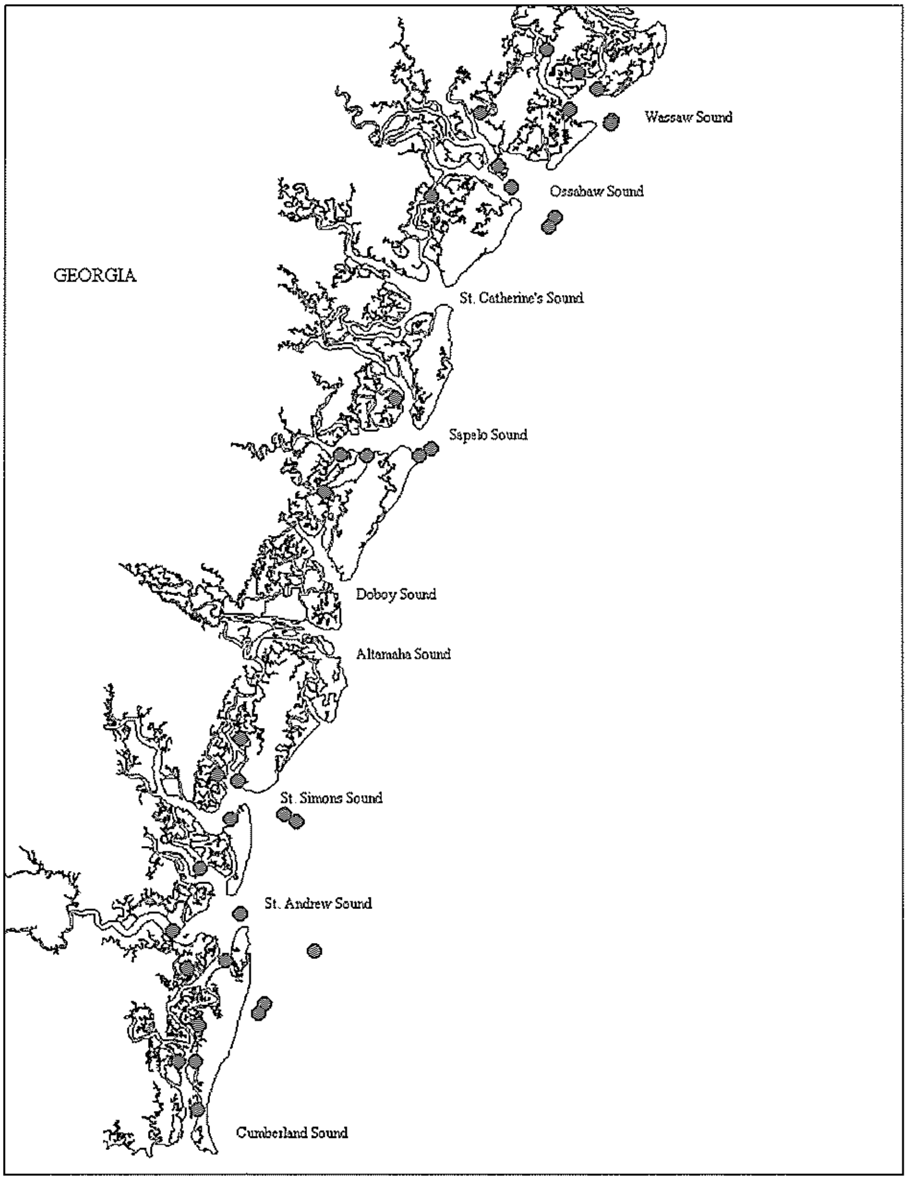

FIGURE 1.—Station locations (n = 36) sampled during monthly assessment cruises conducted in the South Atlantic Ocean by the Georgia Department of Natural Resources' research vessel *Anna* during 1979–2000.

mental data collected in November and December were expected to be negligible.

Rather than test every possible combination of the Beverton–Holt curve with the 16 individual environmental variables representing monthly salinities and water temperatures, two stepwise regression procedures were performed to select the environmental variables that best explained the variation in fall recruit abundance. The first method emphasized maximum improvement in the coefficient of determination R^2. This method evaluates subsets of the variables based on the highest R^2 values. Although this technique allows the analyst to examine a larger variety of models than would be possible in the other stepwise methods, often the optimal model can be overlooked (Montgomery and Peck 1992). To address this issue, we used a second stepwise procedure that evaluated variables already included in the model for significance each time a new variable was added.

TABLE 1.—Mean square errors for models evaluated as potential spawner–recruit relationships for white shrimp in Georgia (1979–2000). Catch per unit effort (CPUE) is measured in pounds per hour trawled. The value in bold italics corresponds to the best single-variable model for estimating fall recruits.

Spawner index	Beverton–Holt model	Ricker model
Fishery-independent indices		
April assessment CPUE	8.8089×10^{11}	2.9064×10^{12}
May assessment CPUE	7.9556×10^{11}	1.2412×10^{12}
June assessment CPUE	***6.5294×10^{11}***	1.3937×10^{12}
Fishery-dependent indices		
May and June commercial landings	8.9322×10^{11}	2.4532×10^{12}

To maintain the final nonlinear model in the simplest form possible, we added the first environmental variable chosen during the multiple-regression procedure to the best-fitting recruitment curve. The final, two-variable model was compared to the original recruitment curve to determine whether the addition of the environmental variable increased the fit of the model. A multiple-regression analysis also was performed to determine whether a linear relationship between spawner indices and environmental variables could explain the variability in fall landings better than the nonlinear form.

In lieu of using R^2 values to compare the effectiveness of the models, we used the mean square error (MSE). This statistic provides the best basis for comparison between models developed from differing assumptions (i.e., nonlinear versus linear, or models fitted with intercepts versus those fitted without intercepts) (Montgomery and Peck 1992).

Results and Discussion

The MSE values for the six fishery-independent spawner index models and the two fishery-dependent spawner index models ranged from 6.5294×10^{11} to 2.9064×10^{12} (Table 1). In general, the Beverton–Holt curves provided better fit for the data than did the Ricker curves. The model with the smallest MSE that best fit the fall recruitment data was the Beverton–Holt curve based on June CPUE as the spawner index. The resulting model is described as follows:

$$R = \frac{\text{CPUE}_{\text{Jun}}}{3.54 \times 10^{-7} \cdot \text{CPUE}_{\text{Jun}} + 7.786 \times 10^{-9}}. \quad (3)$$

Unfortunately, the model did not predict recruit abundance with the degree of precision desired by most fisheries managers (Figure 2). When the best-fitting Beverton–Holt relationship is examined, the reason behind the relatively straight line of the predicted recruitment becomes evident (Figure 3). In the Beverton–Holt model, the ascending arm of the curve is rather steep, which indicates that except for very low values of June CPUE (<0.5 lb/h), the same general yield of fall recruits is predicted. This result suggests that other factors in addition to the general spawner–recruit relationship are affecting white shrimp recruitment success in any given year.

The results from the maximum R^2 improvement technique indicated that September water temperature was the most-predictive single environmental variable, explaining 23.15% of the variation in fall recruitment. When all of the environmental variables were subjected to the stepwise procedure, the resulting model showed that three variables (September water temperature, September salinity, and October water temperature) were successful in explaining a portion of the variation found in fall recruit abundance. However, when the final model was evaluated, September water temperature was dropped, and 44.7% of the variation in fall recruitment was explained by September salinity and October water temperature. Because September salinity was entered into the regression model prior to October temperature, both September salinity and September water temperature were added individually to the best-fitting Beverton–Holt relationship, and the resulting models were examined for overall fit.

Interestingly, the stepwise multiple regression performed with the spawner indices and environmental variables to estimate fall recruitment yielded the same model that was produced when only the environmental variables were used. Because none of the spawner indices were significant in the stepwise regression model, and because a significant spawner–recruit relationship was not detected, three alternate conclusions can be made: (1) fall shrimp landings do not provide a good recruitment index, (2) fall recruitment is driven by effects independent of spawning stock abundance,

FIGURE 2.—Time series showing observed and predicted white shrimp recruit abundance in Georgia waters of the South Atlantic Ocean (1979–2000). Observed values are total commercial landings in fall (August–January). Predicted values are based on the best-fitting Beverton–Holt model (Table 1). Data from the years 1980 and 1982 are omitted; see Methods for explanation.

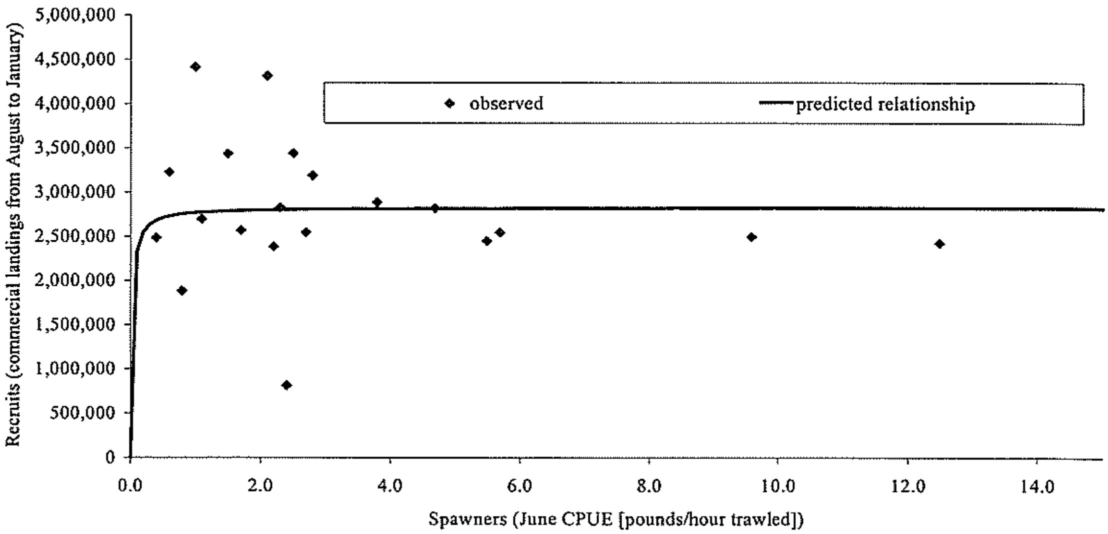

FIGURE 3.—Observed and predicted white shrimp spawner–recruit relationships in Georgia waters of the South Atlantic Ocean (1979–2000). Observed values are total commercial landings in fall (August–January; recruits) versus June catch per unit effort (CPUE; spawners) of assessment surveys conducted by the Georgia Department of Natural Resources. The predicted relationship is based on the best-fitting Beverton–Holt model (Table 1). Data from the years 1980 and 1982 are omitted; see Methods for explanation.

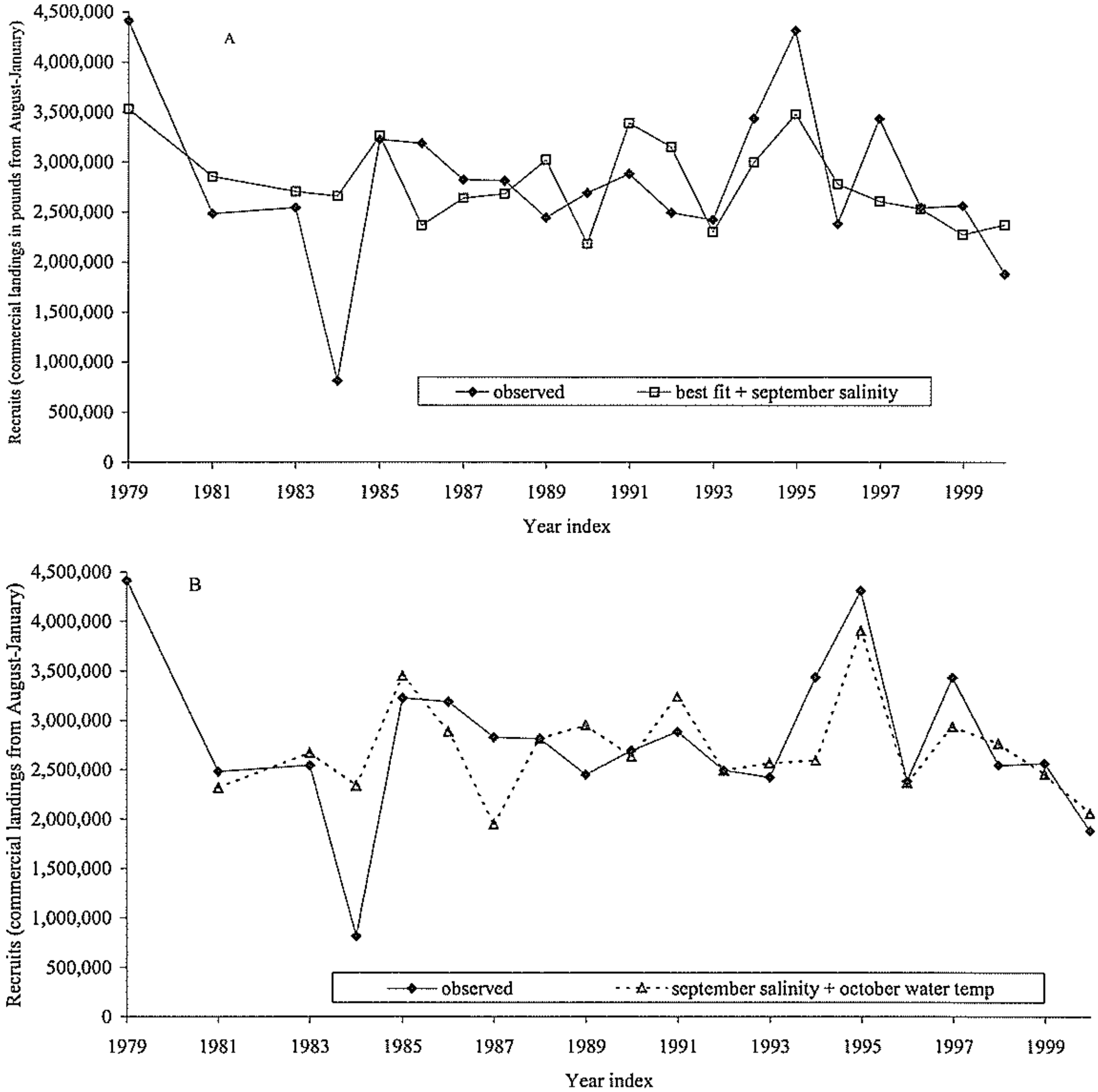

FIGURE 4.—Time series showing observed and predicted white shrimp recruit abundance in Georgia waters of the South Atlantic Ocean (1979–2000). Observed values are total commercial landings in fall (August–January). Predicted values are based on (A) the best-fitting Beverton–Holt model (Table 1) enhanced with the addition of a September salinity variable or (B) a two-variable environmental model that includes September salinity and October water temperature. Data from the years 1980 and 1982 are omitted; see Methods for explanation.

or (3) the spawner indices we used were insufficient.

The best-fitting nonlinear model indicated that September salinity enhanced the fit of the best-fitting Beverton–Holt curve and accounted for 27.67% of the overall variation in fall recruitment (Table 2; Figure 4A). However, the overall best-fitting model was the multiple regression based on September salinity and October water temperature (Figure 4B). The resulting model is described by the equation:

$$R = 2{,}249{,}438 - 119{,}551 \text{ (September salinity)} + 167{,}584 \text{ (October temperature)}. \quad (4)$$

This model explains a larger portion of the variation in fall recruit abundance than did the best-fitting Beverton–Holt model.

Although Lam et al. (1989) successfully used fishery-dependent indices to establish a strong spawner–recruit relationship for white shrimp in South Carolina, we were not able to detect a similar relationship for Georgia white shrimp. Dif-

TABLE 2.—Mean square error (MSE) values for models using environmental variables to predict white shrimp recruits in Georgia (1979–2000). Environmental variables were evaluated with the best fit spawner–recruit curve as well as independently. The value in bold italics indicates the best two-variable model for estimating fall recruits.

Model	Final MSE
Best fit + September water temperature (°C)	6.8869×10^{11}
Best fit + September salinity (‰)	5.2705×10^{11}
September salinity (‰) + October water temperature (°C)	***3.0700 × 10¹¹***

ferences between our results and those of Lam et al. (1989) may stem from the differing management strategies employed by the two states during the period represented by the data. The South Carolina data represented years when the state allowed trawling inside its bays and estuaries, whereas the Georgia data represents years when trawling was not allowed in the sounds. Because South Carolina's commercial fleet was able to cover a larger portion of the actual distribution of white shrimp during the study period, South Carolina landings would be a better indicator of spawner and recruit abundances within the entire population, whereas Georgia's commercial landings are more indicative of abundances of spawners and recruits that are "recruited" into the fishery. Evaluation of fishery-independent indices for both spawners and recruits may yield a better-fitting model.

Other environmental variables related to freshwater input (i.e., river discharge, rainfall), currents, and prevailing winds were not accounted for in the models we examined. The addition of these variables could possibly assist in further explaining variability and improve the resulting fit of the model. Alternatively, the application of other spawner–recruit relationships, such as the models proposed by Shepherd (Bjorkstedt 2000) and Deriso (1980), may better explain the variation in fall white shrimp recruitment in Georgia.

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