Model for white shrimp landings for the central coast of South Carolina

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Abstract.—A stock–recruitment relationship (SRR) was developed for white shrimp *Penaeus setiferus* in the central coastal area of South Carolina. The SRR is a Beverton–Holt-type curve for which May and June commercial fishery landings represent stock and August–January landings represent recruitment. A variable, August salinity in Charleston Harbor, was selected by the stepwise regression process, and it was combined with the Beverton–Holt equation to produce a model that explained 86.8% of the variation in August–January landings. The final model was used to develop a family of SRR curves in which each curve corresponded to a different salinity. This model was sufficiently robust to forecast below-average, average, and above-average fall landings from readily obtainable data collected in spring and summer. These findings support South Carolina's existing management strategy of protecting spring spawners as much as possible after severe winter weather when the brood stock has suffered heavy mortality.

In South Carolina, as in most other coastal states in the southeastern USA, the commercial trawl fishery for penaeid shrimps is composed of two temporally segregated fisheries for the white shrimp *Penaeus setiferus* and the brown shrimp *P. aztecus*. The primary fishery is for white shrimp, which account for an average of about 60% of the annual landings (McKenzie 1981). White shrimp are occasionally caught in large quantities in May and June, the primary spawning season, but the largest landings occur from August to January (hereafter referred to as the fall fishery) when the progeny of the spring spawn are abundant. The majority of the large shrimp (≥120 mm total length), which are not captured by fishermen, move south along the coast and small shrimp remain to overwinter in the estuaries (Lindner and Anderson 1956; Farmer et al. 1978). Annual commercial landings vary considerably; the poorest harvests follow unusually severe winter weather, which results in the nearly total loss of locally overwintering brood stocks (McKenzie 1981).

Shrimp landings have often been related to water temperature. Williams (1969) found a highly significant statistical relationship between the combined shrimp landings of all shrimp species for North Carolina, South Carolina, Georgia, and Texas and heating degree-days (an index of cold weather) for each area. Turner (1977) found an inverse relationship between shrimp yield (kg/hectare) and degrees latitude. Hettler and Chester (1982) noted that a causal relationship of temperature to production (landings) was biologically appropriate and that major variations in pink shrimp *P. duorarum* in North Carolina are probably due to cold induced mortality of overwintering shrimp.

Several researchers have linked rainfall and river discharge to shrimp landings. Hildebrand and Gunter (1953) and Gunter and Hildebrand (1954) showed a relationship between annual harvest of white shrimp in Texas and rainfall of the same year and the two previous years. Barrett and Gillespie (1973, 1975) and Barrett and Ralph (1976, 1977) noted that rainfall and discharge of the Mississippi River, along with water temperature, were important influences on commercial catches of brown shrimp in Louisiana in May. They reasoned that excessive rainfall and river discharge diluted estuarine and nearshore waters below tolerance limits of brown shrimp, thus limiting available optimum nursery habitat. Browder (1985), using multiple-regression analysis, found a strong pos-

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itive relationship between quarterly landings of pink shrimp and average water level (an index of freshwater runoff) of the previous quarter (3 months) for three quarters of the year.

Water salinity has been correlated with commercial harvests of shrimp. Hunt et al. (1980) found that salinity and water temperature in April and May are important variables affecting brown shrimp harvests in Pamlico Sound, North Carolina. Production of brown shrimp in Louisiana has been related to estuarine water salinity and temperature (Ford and St. Amant 1971). McFarland and Lee (1963) found that white shrimp and brown shrimp could osmoregulate over a wide range of salinities but that white shrimp seemed more tolerant of low salinities. Pond rearing studies have shown that salinity may be an important factor in growth and survival of postlarval and juvenile white shrimp (Hysmith and Colura 1976). Thus, it is clear that environmental conditions influence shrimp survival and growth and, ultimately, commercial harvests.

Several studies have produced mathematical models to predict shrimp harvest. Walker and Saila (1986) used environmental variables to produce harvest models for brown and white shrimps caught off Texas and Louisiana. They related ocean currents, river discharge, water temperature, and salinity to shrimp landings. Stepwise regression procedure was used to produce a relatively accurate model (R^2 = 0.84) for white shrimp landings in Louisiana (GMFMC 1980). This model included May–August river discharge and an estimate of commercial fishing effort. Staples et al (1984) developed catch-prediction models for *Penaeus merguiensis* for the Gulf of Carpentaria, Australia. Their best model, which was based on the sum of summer and autumn rainfall, explained 80% of the catch variation of the fishery. Because only rainfall data available prior to the autumn harvest were of predictive value, the model was not of practical use. A second model was developed, however, based on spring and summer rainfall, and it could predict catch with a standard error of ±19% in a year of average rainfall.

An index of catch rates for postlarval shrimp was used in some prediction models. Sutter and Christmas (1983) produced a model for prediction of the brown shrimp harvest in Mississippi waters with multiple linear regression techniques. Their three-variable model was relatively accurate, accounting for 80% of the variability in brown shrimp landings for several years. However, data from 5 years (1967, 1975, 1977, 1979, and 1980) were not included in the analysis because values for the postlarval index were judged too low to be realistic. This index seriously limits the usefulness of a forecast model in some years and can be very expensive in terms of field and laboratory effort. Berry and Baxter (1969) demonstrated that use of a postlarval index was not effective in predicting harvests of brown shrimp in the northwestern Gulf of Mexico.

We sought to develop a model to predict shrimp landings in South Carolina because harvest forecasts are important to user groups and can be used to alter regulations. Commercial and recreational interest-groups often ask for explanations as to why shrimp stocks fluctuate. Understanding the causes of stock variability allows managers to respond to unsubstantiated claims (e.g., overharvesting by recreational fishermen, overharvesting of spawners, water pollution, nutrient overloading) from user groups that are concerned about periodic declines in stock abundance. A model that can explain major shifts in shrimp abundance would be very useful in forestalling needless regulations and legislation. Additionally, businesses tied to the commercial and recreational fisheries often request forecast information when planning budgets and purchasing supplies for the ensuing fishing season. Although most commercial fishermen will fish regardless of projections of stock size, many will plan their fishing strategies (out-of-state travel, targeting other species, purchase of new gear, etc.) around production predictions.

The most useful model should be one that incorporates easily obtained data. Comparison of postlarval catch rates, which are relatively expensive data to obtain, with commercial landings indicates little correlation, although very low catch rates of white shrimp postlarvae precede poor harvests of white shrimp in South Carolina (J. D. Whitaker, unpublished data). Thus, the use of catch rates of postlarvae in most years is considered impractical in a shrimp model. Environmental data, however, are easily obtained and abiotic factors affect growth and survival of shrimp. In this paper, we present a model based on environmental variables and abundances of spawners to describe August–January landings of white shrimp along the central South Carolina coast.

Study Area

The South Carolina coast can be divided into three distinct areas. The southern district has large barrier islands and large open sounds with relatively small freshwater tributaries. The central district, the area examined in this paper, is bordered on the north by the Santee River and on the south by the Edisto River. Like the southern district, the central district has large barrier islands, but most are separated by relatively small inlets. Charleston Harbor is the only large, deep body of water in the central district that is comparable to the sounds of the southern district. Charleston Harbor, however, typically has a much lower salinity than that of the southern sounds (Ballentine 1972; Tiner 1977; Mathews et al. 1980). The northern district, except for the Winyah Bay–Santee Bay area, has very little freshwater discharge, no large estuaries, and relatively few shrimp. In a first attempt to model shrimp landings for South Carolina, we limited our study to the central coastal area (Figure 1).

Data Sources

Data for water temperature and salinity were obtained largely from the Tides and Water Levels Branch of the National Ocean Survey Office (National Oceanic and Atmospheric Administration, Rockville, Maryland). Temperature was measured with a mercury thermometer and salinity was converted from water density measurements obtained with a hydrometer. These were recorded once daily, without regard to tidal stage, at the U.S. Customs House Wharf on Charleston Harbor. Total number of observations per month usually ranged between 15 and 25. Observations were rarely made on weekends. A few data gaps were filled by including supplemental observations determined with a mercury thermometer and induction salinometer for samples taken at the Marine Resources Center of the South Carolina Wildlife and Marine Resources Department (SCWMRD) at Fort Johnson on James Island. Fort Johnson is about 3.2 km across Charleston Harbor from the primary observation site. Because of relatively large semidiurnal tides averaging 1.6 m in Charleston Harbor (NOAA 1985), water salinity can fluctuate considerably, but temperature varies relatively little during a single tidal cycle. Salinity observations taken daily at the same tidal stage would have provided a better indication of nontidally caused fluctuations, but the month-long averages are adequate as a relative index of overall conditions. Salinities measured in Charleston Harbor were highly correlated with salinities measured in smaller nearby creeks.

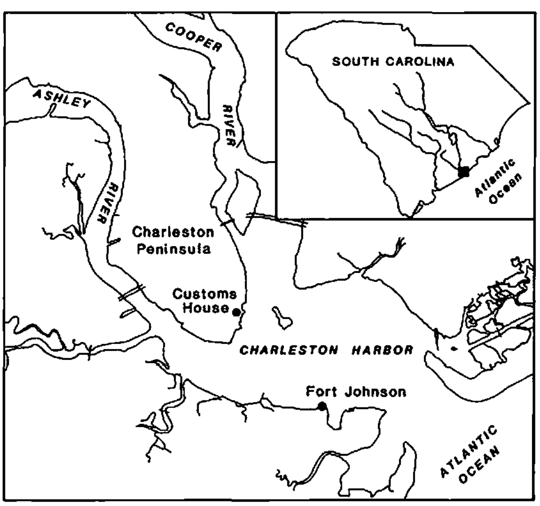

FIGURE 1.—Sampling locations for hydrological conditions in Charleston Harbor. The study area includes the South Carolina coast between the Edisto and Santee rivers.

River discharge data came exclusively from the Cooper River and was measured at the Lake Marion–Lake Moultrie diversion canal near Pineville, South Carolina (USGS 1972–1986). This observation site is about 72 km inland from Charleston Harbor and was the most seaward observation site available for the years included in this study. The average daily flow rate of the Cooper River during the period of the study was 423 m^3/s, the highest discharge of any river in the central district (Bennett et al. 1986). Other rivers within the central district, including the Ashley River, are tidal and drain relatively small coastal areas. The next highest average flow rates occurred in the Santee (96 m^3/s) and Edisto rivers (76 m^3/s); these river mouths are 68 km north and 56 km south, respectively, of Charleston Harbor, at the boundaries of the central coastal district.

Rainfall data were recorded at the downtown Charleston weather station, which is on the Charleston peninsula in Charleston Harbor. Being centrally located in the coastal district, this location should provide an index of coastal rainfall. The Cooper River discharge should reflect the effects of upstate rainfall on estuarine salinity.

Landings data were collected by the Office of Fisheries Statistics of SCWMRD and were limited to those from the central coastal district of South Carolina for the months of August through January of the following year. Occasionally, white shrimp caught elsewhere are landed in the study area. Our observations indicate such landings are unimportant. South Carolina fishermen typically return to port daily and unload shrimp locally. Although some vessels fish in other areas when catch rates are low, a nucleus of vessels remains in the area year-round. Data for fishing effort were not available to calculate catch per unit effort (CPUE) for the entire study period; therefore, landings were used as the dependent variable in our model. Examination of landings, CPUE data for recent years (kilograms per boat per day), and numbers of commercial licenses suggest that fishing effort in South Carolina and total landings are directly related. Examination of recent CPUE data indicates that there is adequate effort to harvest the available resource at or near the level of maximum exploitation every year (A. Applegate, SCWMRD, personal communication). These observations suggest that the fishery is being fully exploited and that landings are a reliable index of stock size. Williams (1969) determined that total landings in North Carolina could serve as a dependent variable as well as his catch-effort index.

TABLE 1.—Mean catch rates of white shrimp during 1976–1977 in double-rigged 6.1-m bottom trawls towed for 30 min at five locations in Charleston Harbor. Weights are for whole white shrimp. Dead shrimp (mean number per sample) had been obviously dead before collection and were in a state of decomposition.

Date	Live shrimp (kg)	Mean number of dead shrimp	Mean bottom temperature (°C)
Dec 1, 2	17.9	0	11.5
7, 10	19.6	0	11.4
15, 16	23.7	0	12.1
21, 22	7.0	0	9.5
29, 30	33.6	0	9.4
Jan 4, 5	5.0	0	8.5
12, 13	2.3	0	7.2
17, 18	0.3	3.4	5.6
26, 27	0	1.8	5.9
Feb 1, 2	0	4.0	6.4
7	0	0	6.7
14, 15	0	0	9.5
23, 24	0	0	10.8

Model Development

There are several well-known linear regression methods: multiple linear regression, all-possible-subsets regression, and stepwise regression. Multiple regression is not suitable in this case because one does not know, a priori, what variables should be included in the model. The all-possible-subset regression procedure was not used because the number of possible variables greatly exceeded the number of cases. We elected to use stepwise regression procedure, which examines the significance of each variable at each step, selects the "best" variable based on F-statistics, and deletes any previously selected variable subsequently found to be insignificant (program 7R from BMDP 1983).

Peak immigration of postlarval white shrimp into South Carolina's estuaries occurs from June through August (Bearden 1961). During these months, juvenile shrimp are abundant in the tidal streams, salt marshes, and other shallow estuarine areas, where they grow rapidly (McKenzie 1981). Therefore, we chose to examine environmental data for the months of May through August. Environmental variables considered for spring and summer of 1970–1984 are monthly average water temperature, monthly average salinity, total monthly rainfall in Charleston, monthly average river discharge for the Cooper River, and 2-month averages (May–June, June–July, July–August) of water temperature and salinity.

Severe winter temperatures have been related to high mortalities of overwintering white shrimp in South Carolina and, less frequently, in Georgia (McKenzie 1981; Daigle 1984). Experimental sampling during the severe winter of 1976–1977 showed a decline in weekly catch rates with decreasing water temperature and zero catch rates in the spring (Table 1). Sampling during other unusually cold years has provided similar results. Following severe winters (1976–1977, 1977–1978, 1980–1981, 1983–1984), South Carolina's fall landings were 12–43% of the 1970–1984 average. We believe that severe winters deplete the spring spawning stock and contribute to poor recruitment and low fall landings. Lindner and Anderson (1956) reported that there were few adult white shrimp along the South Carolina and Georgia coasts during spring following the severe winter of 1939–1940. South Carolina's white shrimp landings in 1940 were 46% of the previous 2-year average, a decrease that Lindner and Anderson attributed to cold kill of overwintering shrimp and few returning migrant shrimp. White shrimp that had migrated south in fall and early winter were heavily fished in Florida waters. The intense fishing effort off Florida has continued, and it is thought that few potential spawners survive to migrate northward into South Carolina waters (McKenzie 1981).

Hettler and Chester (1982) also demonstrated a relationship between winter water temperature and subsequent landings of pink shrimp in spring and early summer. Because overwinter conditions affect numbers of spawning shrimp in spring (Lindner and Anderson 1956), we included variables for winter conditions for December through March: monthly average water temperature, 2-month average water temperature (December–January, January–February, February–March), and temperature-days, which is the total number of days in which Charleston Harbor water temperature was 8.5°C or less. To more directly examine spawner abundance, we included indexes of May and June spawners: (1) SCWMRD catch-per-unit-effort data for white shrimp collected in estuarine sampling in April (CPUE), and (2) total landings of white shrimp during May and June in the central district.

Examination of size-frequency data from landings and field sampling clearly showed that small shrimp captured in August were the progeny of the spring spawning stock, Thus, we included August landings in our fall landings (dependent variable). For the period of the study, white shrimp landings for the month of August averaged only 6.6% (SD = 4.3; range = 0.4–12.7) of the August–January totals.

When all of the previously described environmental variables were included in the stepwise regression procedure, water salinity in August and temperature-days were the only significant ($P < 0.05$) variables for estimating landings. The resulting model is ($R^2 = 0.774$)

$$Y = 1642.84 - 53.55S_A - 8.21\text{TD}; \quad (1)$$

Y = fall (August–January) commercial shrimp landings (kg);
S_A = salinity (‰) for August;
TD = temperature-days.

Salinity in August accounted for 60.4% of the variability in fall landings and TD accounted for an additional 17%. The deviations between observed and predicted landings ranged from −567 to 58%. We judged that this model was not adequate for predicting fall landings and explored other methods that included an index of spawner abundance.

Even though the model from the stepwise-regression process did not fit the observed landings well, it identified two of the more important variables: August salinity and the number of days when water temperature falls to or below 8.5°C (temperature-days). Spring landings have a nonlinear and reciprocal (inverse) relationship with temperature-days (Figure 2). Once the number of temperature-days exceeds about 18, further cold weather has little effect because all shrimp are already dead. We believe that fall white shrimp production is related to cold weather of the previous winter only through the quantity of spring spawners that survived the winter. It could be argued that winter conditions may have some other relationship to fall production, such as an effect on

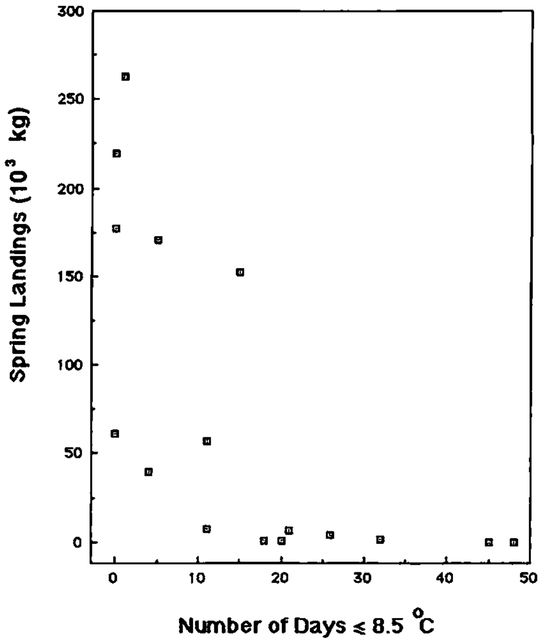

FIGURE 2.—Spring (May and June) white shrimp landings (tonnes, heads off) versus number of days during the preceding winter in which water temperature was 8.5°C or less.

potential predators or prey, or perhaps an effect on nutrient levels. We have no data to support or dispute this.

We investigated the possibility of a spawner-recruit relationship (SRR) using spring landings of white shrimp to represent spawner abundance and fall landings to represent recruitment. The Simplex optimization procedure (Nelder and Mead 1965) was used to estimate the parameters of the nonlinear Beverton–Holt (1957) curve by minimizing the following criterion:

$$\text{SS} = \sum_{I=1970}^{1984} [Y_{\text{cal}}(I) - Y_{\text{obs}}(I)]^2;$$

SS = sum of squares;
$Y_{\text{obs}}(I)$ = fall white shrimp landings of the Ith year;

$$Y_{\text{cal}}(I) = \frac{\alpha \text{Sp}(I)}{1 + \beta \text{Sp}(I)}.$$

Y_{cal} is the Beverton–Holt equation; Sp(I) are spring white shrimp landings (spawners) and α and β are constants. The resulting model is

$$Y_{\text{cal}} = \frac{272.83\text{Sp}}{1 + 0.3828\text{Sp}}. \quad (2)$$

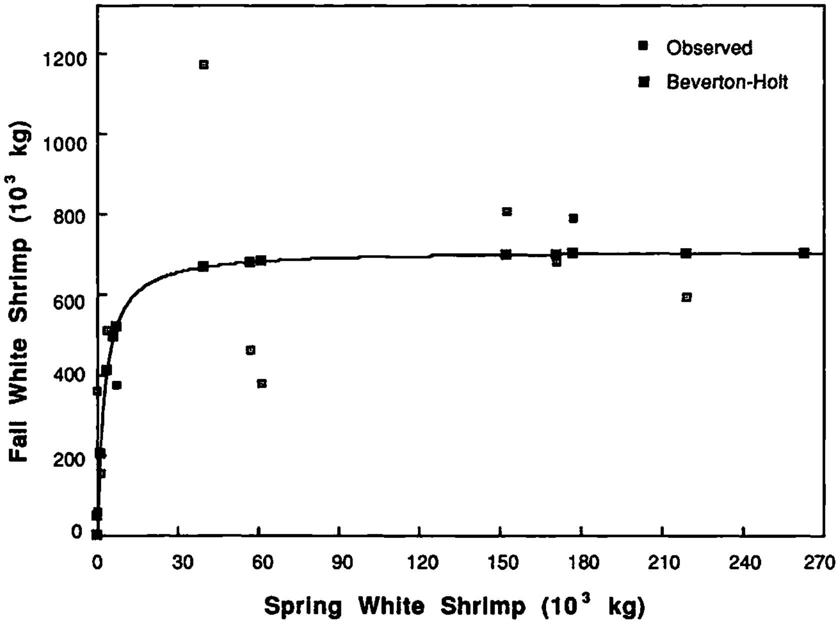

FIGURE 3.—A computer-generated Beverton–Holt curve computed from observations of spring and fall landings (tonnes) of white shrimp.

An SRR curve was created from this model, which accounted for 54.1% of the variability in fall landings (Figure 3). Observed and calculated values were close in only 7 of 15 years examined (Figure 4), and there were unacceptably large discrepancies in several years.

Because August salinity was the first variable selected in the stepwise regression process, it was combined with the Beverton–Holt equation to produce a new model:

$$Y_{cal} = A + BS_A + \frac{\alpha \text{Sp}}{1 + \beta \text{Sp}}.$$

The parameters A, B, α, and β were estimated with the Simplex nonlinear optimization process, resulting in

$$Y_{cal} = 119.7 - 47.62S_A + \frac{140\text{Sp}}{1 + 0.3309\text{Sp}}. \quad (3)$$

This model explained 86.8% of the variability in fall landings. Observed and calculated values were relatively close for all years of the study (Figure 5). Values of August salinity for 1970–1984 and 1985 were then used in equation (3) to produce a family of Beverton–Holt spawner–recruit curves (Figure 6).

Discussion

A model developed by Walker and Saila (1986) for white shrimp in the vicinity of the Texas–Louisiana boundary showed that landings were positively correlated with river discharge, and that northwest winds (northeast Ekman transport) during the spring and summer appeared to be correlated with decreased landings. They speculated that a northeasterly transport of larvae during the spawning season would carry these shrimp away from the estuarine nursery areas. The transport conditions for the area were also noted to affect other factors, such as average tidal levels in the marshes, which can influence growth and survival. Zimmerman and Minello (1984) observed that high seasonal tides on the Texas coast facilitated access of shrimp to vegetated habitat in marshes. Because white shrimp spawn relatively close to shore in South Carolina (McKenzie 1981), and perhaps inside some sounds and bays, we believe that the relatively strong tidal currents are usually much more important in transporting larvae and postlarvae than wind-driven currents. Water levels in the marshes are also largely the result of tides and not wind. For these reasons, no wind data were examined in this study.

We find that water salinity is inversely related to white shrimp landings. Barrett and Gillespie (1973) noted that inshore shrimp-fishing grounds in Louisiana included about 809,400 hectares during years of high rainfall and high river discharge but increased to 1,153,400 hectares during

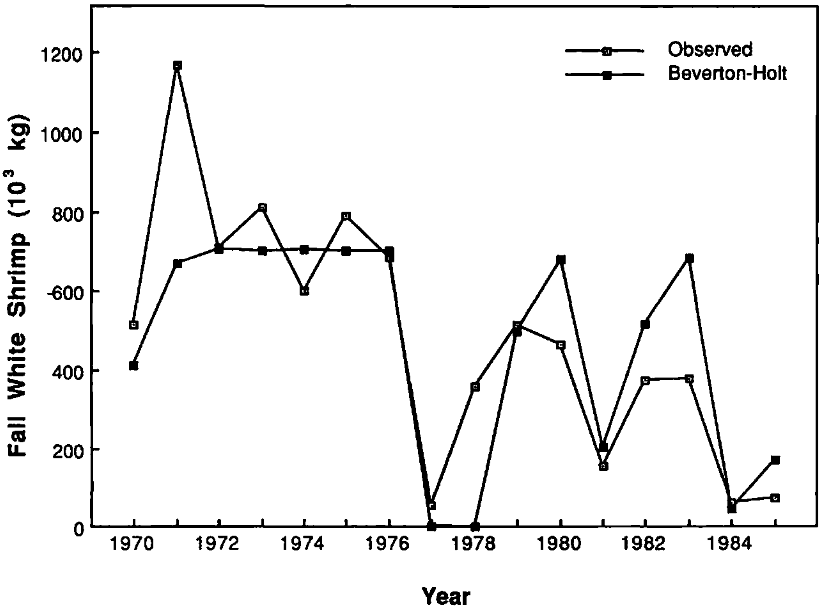

FIGURE 4.—Observed fall landings (tonnes) of white shrimp and calculated landings based on the Beverton–Holt equation.

years of high salinity. Although Louisiana's brown shrimp production is negatively related to rain and discharge, the opposite may be true in South Carolina where, without the presence of a major river system such as the Mississippi River, increased rainfall and river discharge may help reduce salinities to optimal levels and may expand available nursery habitat. Browder (1985) noted that freshwater inflow can have positive or negative effects on young fish and shellfish depending on the characteristics of the particular estuary and the volume of the freshwater inflow. She suggested that changes

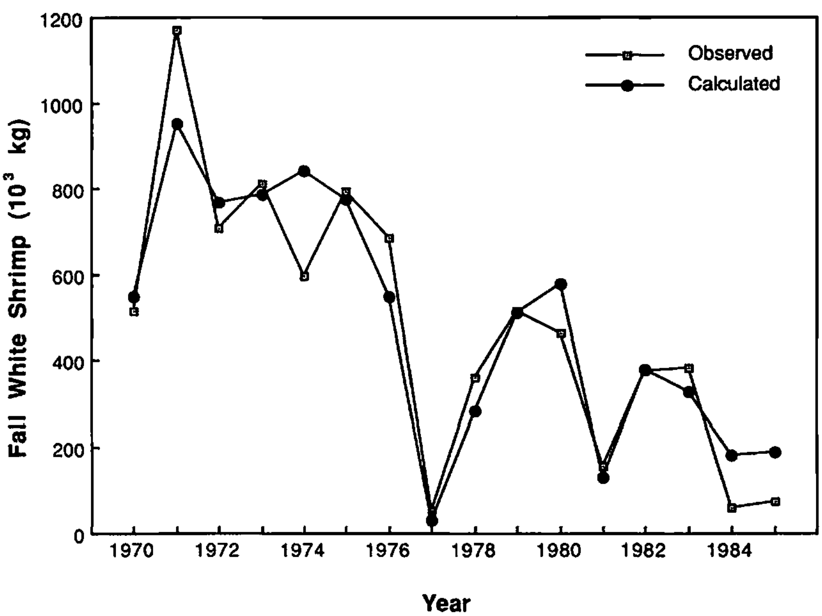

FIGURE 5.—Observed fall landings (tonnes) of white shrimp and calculated landings from the recruitment forecast model (equation 3).

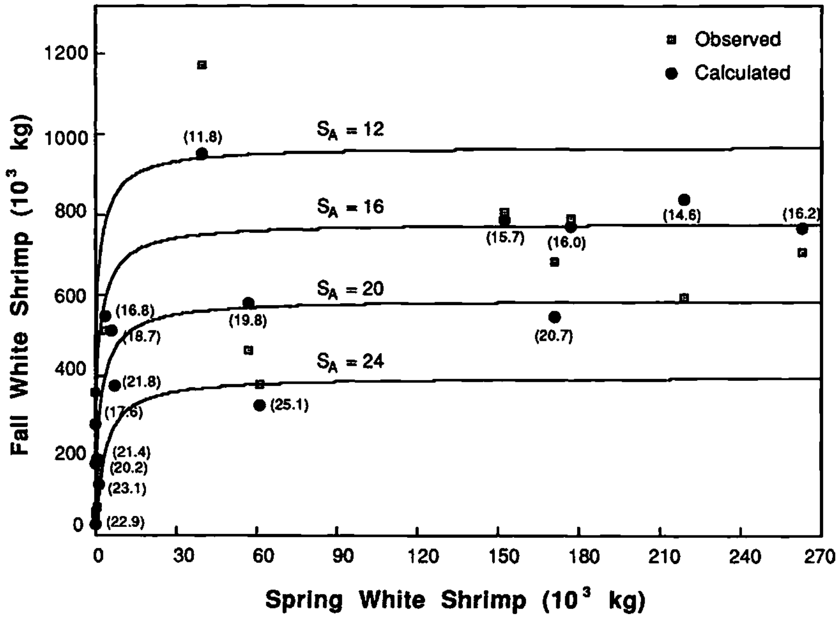

FIGURE 6.—A family of computer-generated Beverton–Holt curves for white shrimp, each curve representing a different salinity (S_A, ‰). Calculated values for fall landings (tonnes) of white shrimp are located directly above or below observed values. The numbers in parentheses are observed August salinity values (‰).

in water-flow patterns may reduce the area of suitable bottom covered by water in which certain salinities or other conditions are favorable to estuarine fauna. Penn and Caputi (1986) developed a model for *Penaeus eculentenus* in Exmouth Gulf, Western Austrlia that included an adjustment for rainfall.

The relationship between salinity per se and white shrimp growth and survival is unclear. Johnson and Fielding (1956) demonstrated good survival in high salinities (34‰). Zein-Eldin (1963) also found that postlarval white shrimp can survive and grow in a wide range of salinities. Subsequent examination of temperature–salinity combinations, however, showed that postlarval white shrimp produced twice as much tissue at intermediate salinities than at salinities of 25 and 35‰ (Zein-Eldin and Griffith 1969). Hysmith and Colura (1976) demonstrated that pond-reared white shrimp had greater growth rates at 15‰ than at 7 and 21‰ in ponds. Several field studies have shown that white shrimp are often more abundant in the lower salinity waters of estuaries (Gunter 1950; Williams 1955; Gunter et al. 1964; Loesch 1965). Our study does not show cause and effect, but it gives strong circumstantial evidence that salinity or some factor governed by or related to salinity is indeed important for growth and survival of white shrimp during their estuarine life phase.

May–August temperature variables did not appear to be important, probably because water temperature is above 20°C by the time postlarvae enter the estuaries (Bearden 1961). Based upon rearing studies of postlarval brown shrimp, Zein-Eldin and Griffith (1966) suggested that temperatures greater than 20°C bring about relatively minor increases in the time required to complete postlarval development. In a laboratory study of growth of postlarval white shrimp, Zein-Eldin and Griffith (1969) found similar growth rates for shrimp reared at temperatures between 25 and 32.5°C. They noted that white shrimp are not abundant in Texas estuaries until water temperatures are well above 25°C and that few enter the estuaries as late as November when temperatures are below 20°C.

We have demonstrated that a spawner–recruit relationship exists for white shrimp in South Carolina. However, a single Beverton–Holt relationship is not adequate to explain the variability of recruitment. On the other hand, a family of curves, each curve representing a different August salinity, explained 86.8% of the variation. Garcia (1984) suggested that a flat relationship of a Beverton–Holt type may exist for shrimp, but that environmental variability masked the relationship. This appears to be the case for white shrimp in South Carolina. Several researchers have proposed that a Beverton–Holt-type relationship would be most likely for shrimp (Garcia 1983, 1984; Penn 1984; Ye 1984) and that a family of curves, each curve corresponding to a given set of environmental conditions, would be better than a single curve (Rothschild and Gulland 1982; Gulland and Rothschild 1984). A previous effort to determine a spawner–recruit relationship for white shrimp in the Gulf of Mexico was unsuccessful (Rothschild and Brunenmeister 1984). In our study when spring landings (spawners) in South Carolina were less than about 10,000 kg, fall recruitment was poor (Figure 6). When landings exceeded this value, low salinity in August improved fall recruitment.

Perhaps for South Carolina, fishermen do not harvest enough brood stock to result in decreased recruitment to the fall fishery, but it is apparent that severe winter weather can reduce stock size at this latitude to the point of being inadequate. Poor fall landings of white shrimp following severe winters have convinced regional managers that mortality of the overwintering brood stock results in very low quantities of spawners and subsequent poor recruitment (McKenzie 1981; Daigle 1984). However, the effects of poor recruitment resulting from severe winters can be offset to a limited extent by favorable environmental conditions during the summer. On the other hand, fewer spawners may be required to produce good fall harvests in years of optimal environmental conditions during late spring and summer.

The present study indicates that spawner abundance, at least in years following severe winters, and environmental conditions can be important for shrimp production in South Carolina. This study also supports South Carolina's existing management strategy of protecting spring spawners to the extent possible after severe winter weather destroys a large percentage of the brood stock. The model developed herein also can be used to predict below-average, average, or above-average landings for the central coast of South Carolina.

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