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Abstract

White shrimp (*Litopenaeus setiferus*) landings in Louisiana display substantial intra- and inter-annual variability. This variability reflects the stochastic impacts of environmental factors that influence growth, mortality, and subsequent survival in a given year, a situation that frustrates attempts by fisheries managers to predict future abundance. We developed a recursive three-equation model for predicting Louisiana white shrimp abundance and subsequent catch based on lagged life-stage counts and environmental parameters such as temperature, river discharge, and cumulative wetland loss. The estimated model demonstrated a significant and positive relationship between early life stage abundance and temperature and salinity. At the same time, wetland loss and high river discharges were related to lower abundance. Biological factors such as numbers of juvenile shrimp at early life stages predicted late juvenile abundance, with a similar relationship existing between late juveniles and adult catch per unit effort (CPUE).

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1. Introduction

Accounting for the intra- and inter-annual variability in fisheries landings or catch per unit effort (CPUE) is one of the most frustrating problems facing fisheries managers. This has been especially true for the Gulf of Mexico white shrimp (*Litopenaeus setiferus*) fishery in Louisiana, where inshore landings have ranged from a low of 9.97 million kilograms in 1978 to a high of 27.21 million kilograms in 1986. High variability in landings is a classic feature of penaeid shrimp fisheries around the world, and it presents a challenge to the development of predictive models (rather than finely tuned hindcasting models) of shrimp abundance. This variability can be ascribed to a number of biological and environmental factors that influence growth,

mortality, and subsequent survival in a given year. But, given the large quantity and high value of the Gulf of Mexico landings, there has been surprisingly little published research on the relationship between white shrimp harvests and environmental or biological parameters.

There are three general types of models that have been used in attempts to predict the annual abundance of commercial-size penaeids. The first relates adult abundance to biological factors such as the abundance of earlier life-stages. An example of this approach is the Baxter Bait Shrimp Index (BBSI) model for brown shrimp in Galveston Bay (Baxter et al., 1988). The second modeling approach relates abundance to environmental factors such as temperature (air and/or water), precipitation, river runoff, frequency of favorable wind trajectories, water levels, and/or area of available habitat. An example of this approach is the documented correlation of rainfall and annual catches of white shrimp in Texas (Hildebrand and Gunter, 1953; Gunter and Edwards, 1969). Interestingly enough, those same authors were unsuccessful in relating Texas brown shrimp harvests to environmental factors. The third approach involves stock-recruitment models which attempt to relate the abundance of reproductive-age shrimp in one generation to the number of recruits entering

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the fishery in the next generation. For penaeid shrimp, models that use the abundance of an earlier life-stage as a predictor tend to be statistically superior to models based on environmental indices (Garcia, 1983).

This paper describes a recursive, three-equation white shrimp abundance model for Louisiana that covers the period 1970–1997 and combines the features of previous modeling approaches. In the first equation, monthly estimates of early juveniles are regressed on a suite of environmental variables. In the second equation, monthly estimates of late juveniles are regressed against a suite of environmental variables and current and lagged estimates of early juveniles. In the last equation, adult abundance, estimated as monthly reported white shrimp catch standardized by effort, is regressed against a suite of environmental factors and current and lagged estimates of late juveniles. Iterative substitution of the three equations after estimation allows one to examine the full impact of any specific environmental variable, even one directly affecting only the early juvenile stage, on any subsequent life stage. This provides a mechanism for simulating the resultant changes in estimated adult abundance associated with varying any exogenous (independent) variable in the model, and it also provides the information needed to calculate the population elasticities associated with any exogenous variable. In turn, this predictive and elasticity information can be used in determining potential harvests and the required management actions in the fishery.

2. Materials and methods

2.1. Study area and species

The Gulf of Mexico (GOM) accounts for approximately 70% of the U.S. commercial production of shrimp, with Louisiana being the largest contributor among the Gulf States. The two primary species harvested in Louisiana are white shrimp and brown shrimp (*Farfantepenaeus aztecus*). During the 1990–2001 period, Louisiana's commercial production of white shrimp averaged 21.77 million kilograms (head-on), while landings of brown shrimp averaged 22.68 million kilograms (head-on). The dockside value of these landings averaged \$157 million annually, with white shrimp production representing almost 60% of this value.

White shrimp in the northern Gulf of Mexico have a relatively complex life history over a generation time of 9–12 months. Demersal eggs are spawned offshore, generally in 7–30 m water depths (Lindner and Anderson, 1956; LDWF, 1992). The spawning season off Louisiana is believed to encompass the months of April to October, with peak activity occurring from May to August. Once hatched, white shrimp pass through a series of planktonic stages over a period of 10–12 days (Garcia, 1985). Postlarval white shrimp then recruit to Louisiana estuaries from June through August (Gaidry and White, 1973; White and Boudreaux, 1977) in a process thought to be aided by selective tidal transport (Hughes, 1969; Duronslet et al., 1972; Lochmann, 1990). For the most part, white shrimp postlarvae move into shallow water habitats such as open bays, salt marshes, seagrass

beds, and shallow, sandy-mud, muddy or peaty intertidal regions, although their affinity for marsh edge and flooded marsh surfaces is not as strong as it is with brown shrimp (Zimmerman and Minelo, 1984). Within these marsh habitats they metamorphose into juveniles, which aside from the lack of functional reproductive systems are morphologically similar to the adults. As the shrimp grow over a period of 3 months they move into progressively deeper water (Baxter et al., 1988). Emigration offshore as juveniles and/or subadults often begins in conjunction with declines in estuarine salinity (Rothlisberg et al., 1985; Staples and Vance, 1986), temperature (Matylewich and Mundy, 1985), and/or changing lunar phase (King, 1971), and typically lasts from September through November. Progressive movement into deeper waters continues as the shrimp grow, complete sexual maturation, and then spawn.

2.2. Biological predictors of abundance

Most biological-based forecasting tools have utilized the abundance of estuarine-resident or emigrating juvenile shrimp to predict adult landings offshore because of the close temporal and spatial association of juveniles and harvested sub-adult/adult shrimp. Baxter (1963) demonstrated that cohorts of post-larvae brown shrimp could be identified in subsequent juvenile and adult fishery samples and ultimately in commercial landings, suggesting that abundance during spring immigration could be used as a tool to forecast subsequent landings early enough for the harvest industry to adjust. Several other studies have shown a positive relationship between penaeid post-larvae and juvenile abundances (Christmas et al., 1966; Subrahmanyam and rao, 1970; Roessler and Rehrer, 1971), but subsequent analyses have not always supported this relationship (DeLauncey et al., 1994). Results from Louisiana suggested that there was no significant relationship between brown shrimp post-larval abundance and juvenile abundance (St Amant et al., 1965). Berry and Baxter (1969) also examined 7 years of brown shrimp post-larval data and could not find a predictive relationship between post-larval CPUE and the bait (juvenile) or offshore commercial CPUEs (see Table 1 for a summary of predictive studies).

More recent investigations have generated renewed interest in biological-based predictive models (Sutter and Christmas, 1983; Baxter et al., 1988). Environmental and Post-larval Model (MEP) is a hybrid climatic-biological model with impressive predictive power that incorporates an index of post-larval abundance and measures of temperature, precipitation and water height. A recent paper by DeLauncey et al. (1994) describes a predictive model for white shrimp that also has significant predictive power and a novel predictive outcome—numbers of adults are predicted rather than the traditional kilograms landed.

Juvenile indices have been employed for management purposes in several fisheries (Table 1). The BBSI is the most well documented use of juveniles as predictors of offshore brown shrimp commercial catch, and for a number of years its predictions were within $\pm 10\%$ of actual landings. Barrett and Gillespie (1973) demonstrated that the abundance data (1954–1972) for juvenile brown shrimp in Barataria and

Table 1
Summary of predictive models used to estimate commercial shrimp population

Predictor	Fishery	Location	Species	R ²	Authors
Climatic predictors					
Mean precipitation for $t - 2$ years or mean precipitation for current + $t - 2$ years	Annual offshore landings (lbs)	TX	<i>L. setiferus</i>	0.44–0.49	Hildebrand and Gunter (1953), Gunter and Edwards (1969)
Summer monsoonal precipitation	Annual landings (MT)	Gulf Carpentaria, Australia	<i>P. merguensis</i>	0.75	Staples (1985)
July–December rainfall of previous year	Annual estuarine landings (kg)	Patos Lagoon, Brazil	<i>P. paulensis</i>	0.49	Castello and Möller (1978)
January–March Guayas River Flow	Gulf of Guayaquil Trawl CPUE (MT/boat)	Gulf Guayaquil, Ecuador	<i>P. vannamei</i>	0.52	Cun and Marin (1982)
Zambezi River Discharge from preceeding August–March (km ³)	Coastal CPUE September–August (TI > 13.5 cm) (n/hr)	Sofala Bank, Mozambique	<i>P. indicus</i>	0.80	Da Silva (1986)
Hours Barataria Bay water temperature below 20 °C after April 8	May inshore landings Barataria–Caminada Bay (lbs)	LA	<i>F. aztecus</i>	0.69 ^a	Barrett and Gillespie (1973), Barrett and Ralph (1977)
Mean water temp of the two coldest consecutive weeks in Newport River estuary	February–July offshore landings (kg)	NC	<i>P. duorarum</i>	0.82	Hettler and Chester (1982)
Biological predictors					
Numerical abundance of emigrating juveniles	New recruits into Tortugas grounds fishery	FL	<i>P. duorarum</i>	^b	Yokel (1969)
April 25–August 31 Galveston Bay Juv. Bait Shrimp Index	Offshore commercial landings (lbs)	TX	<i>F. aztecus</i>	0.72 ^c	Berry and Baxter (1969), Caillouet and Baxter (1973)
May juveniles catch in Caminada and Barataria Bays (lbs)	Annual offshore catch (lbs)	LA	<i>F. aztecus</i>	0.88	Barrett and Gillespie (1973)
May juveniles catch in Caminada and Barataria Bays (lbs)	Combined offshore + inshore catch (lbs)	LA	<i>F. aztecus</i>	0.92	Barrett and Gillespie (1973)
Postlarval Abundance February–July	Commercial catch in Mississippi sound (lbs)	MS	<i>F. aztecus</i>	Not stated	Christmas et al. (1966)
Postlarval Abundance Index	Offshore fall commercial numbers landed × 10 ⁶ shrimp	SC	<i>L. setiferus</i>	0.79	DeLauncey et al. (1994)

^a Qualitative Index: ≥ 100 h = low production; 33–99 h = average production; < 33 h = high production. We calculated the relationship from their data to be $R^2 = 0.69$.

^b Correlation listed as “good” but not calculated.

^c Bait Shrimp Index: Catch (10⁶ lbs tails) = 14,348 + 0.276 Bait Shrimp Index ($R^2 = 0.72$, $n = 18$) Index = mean CPUE (lbs* h fished⁻¹) from Galveston Bay’s bait shrimp fishery. Bait shrimp landings and effort data are obtained from cooperating bait shrimp dealers and adjusted for brown shrimp content on the basis of 1 qt samples. The index is then the average of seven weekly averages of CPUE by bait fishermen from five regions of the bay from April 25 to June 12 each year.

Caminada Bays, Louisiana could be used to predict the inshore and combined inshore/offshore brown shrimp catch. Both the Galveston and Louisiana examples demonstrate the potential utility of using juvenile indices to predict offshore landings.

2.3. Environmental predictors of abundance

While under normal conditions biological factors may have the biggest impact on abundance, environmental factors can be important at the extremes (Garcia and Le Reste, 1981). Predictive models that utilize environmental factors typically depend on one or two driving variables which presumably control the survival of earlier life stages. For example, penaeids are subtropical species whose range extends into warm temperate waters, but temperatures below 18–20 °C are suboptimal for growth (Witzell and Allen, 1982) and may have a measurable effect on production if temperature drops below 20 °C for a large part of the year (Staples et al., 1985). Coastal precipitation and air temperature will also help determine the prevailing estuarine

salinity and temperature regimes, and thus the growth, movement and survival of shrimp (Witzell and Allen, 1982). Although cold fronts and storms have been implicated in shrimp mortality, these events are uncommon and may not be important to Louisiana white shrimp mortality during summer (Minelo and Zimmerman, 1991). The heavy precipitation associated with tropical storms, however, can reduce salinities to near zero in a few hours and flush organisms out of estuaries (Forbes and Hay, 1988).

Because of these environmental relationships, attempts have been made to develop climatic-based predictor models for a number of geographically diverse penaeid fisheries (Table 1). For example, the Louisiana Department of Wildlife and Fisheries (LDWF) has demonstrated a relationship between water temperature and Louisiana brown shrimp production, suggesting that May estuarine landings are related to the number of hours that April water temperatures are below 20 °C (Barrett and Gillespie, 1973). Barrett and Ralph (1977) noted that brown shrimp landings were low during wet years in Louisiana, even though the correlations with precipitations were not very high.

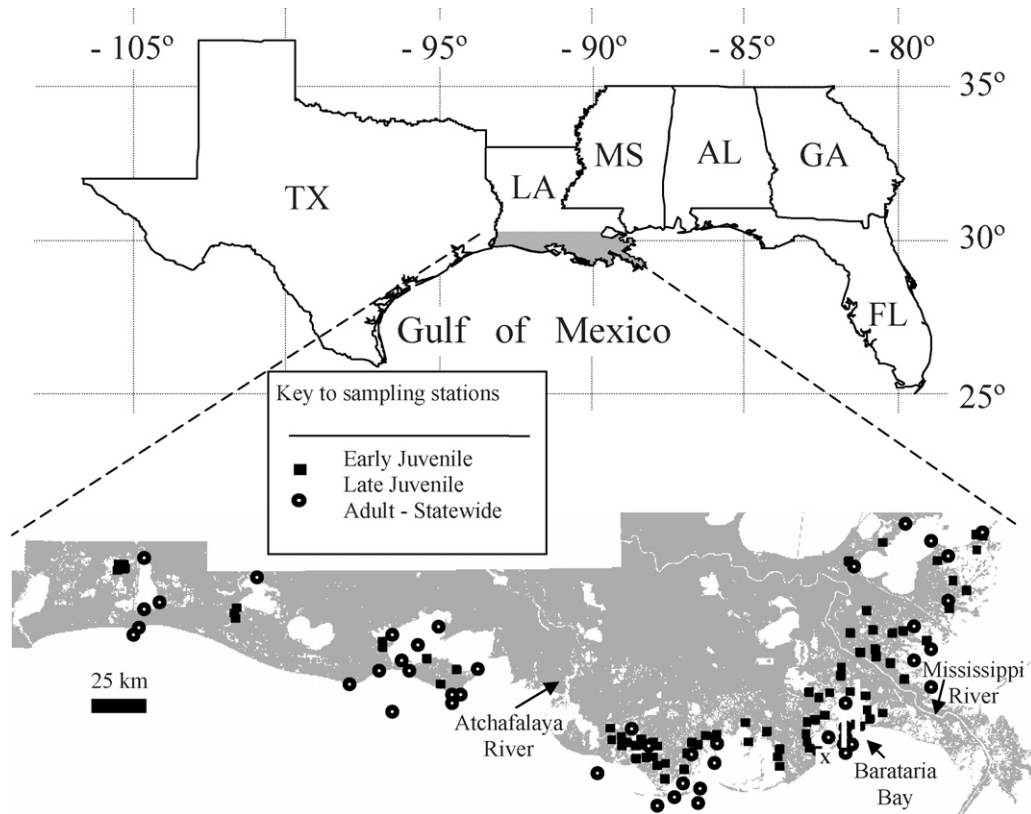


Fig. 1. Map of the northern Gulf of Mexico and coastal Louisiana, U.S.A., showing an example of Louisiana Department of Wildlife and Fisheries sampling stations for white shrimp. Stations varied slightly from year to year, and the locations shown in this map represent stations sampled in a typical year. Open-water areas are shown in white; early juvenile sampling stations are indicated with a solid square; and late juvenile sampling stations are indicated with an open circle (after Haas et al., 2001).

Presently, LDWF utilizes both temperature and precipitation data to estimate the percentage of available nursery habitat acreage to assist them in forecasting subsequent landings. Even large-scale climatological forces such as la Niña and El Niño–Southern Oscillation (ENSO) events have been related to precipitations and estuarine water levels, and, therefore, the frequency of Louisiana marsh inundation (Childers et al., 1990). The 1987–1988 la Niña event was associated with one of the lowest CPUE shrimp years on record.

In addition to the basic environmental variables, long-term studies have suggested a direct relationship between available wetland habitat and offshore shrimp landings. Numerous examples of reductions in offshore and artisanal landings in response to reclamation of wetlands have been documented (Pauly and Ingles, 1988; Turner, 1992, 1997). While it is not clear what constitutes quality habitat for many species of penaeid shrimp, habitat quality and quantity are thought to be two of the factors influencing shrimp harvests in the long-run. Each species appears to be associated with a particular estuarine habitat type. For example, quantitative drop-sampling along the Gulf of Mexico has demonstrated that brown shrimp are associated with emergent aquatic vegetation (Minelo and Zimmerman, 1985; Minelo et al., 1989; Zimmerman et al., 1984). High habitat specificity may either enhance growth because of local food availability or reduce mortality by offering structural refugia from predators (Minelo and Zimmerman, 1985, 1991). Juvenile

white shrimp, however, do not appear to have the same affinity as brown shrimp for marsh edge (Zimmerman and Minelo, 1984; Minelo and Zimmerman, 1985).

2.4. Data

The shrimp fishery in the GOM is monitored by both fishery-independent and fishery-dependent methods. Fishery-independent data has been collected over the years at several coastal locations by the LDWF (Fig. 1). A detailed description of the data collection procedures can be found in the Marine Fisheries Division Field Procedures Manual (LDWF, 1992). From this information we assembled a dataset that included 28 years (1970–1997) of stage-specific white shrimp abundance estimates and a suite of concurrent environmental variables. Most data were specific to Louisiana, but are representation of the northern Gulf of Mexico since, on average, more than 60% of Gulf of Mexico white shrimp is harvested and landed in Louisiana. CPUE (Griffin et al., 1997) was used as an index of relative abundance at the three life stages—early juvenile white shrimp from shallow marshes (number of shrimp per 10 min 1.8 m otter trawl with 9.52 mm mesh); late juveniles from open bays, sounds and lakes (number of shrimp per 10 min 4.8 m otter trawl with 19.05 mm mesh); and monthly indices of adults abundance from reported industry catches (not landings) in Louisiana (both inshore and offshore) adjusted by the amount of effort.

Table 2
Variable description

Label	Definition and measurement units	Source
NUMSIX (early juveniles)	Number of shrimp per 10 min 1.8 m otter trawl with 9.52 mm mesh size	Louisiana Department of Wildlife and Fisheries
NUMSIX _t	NUMSIX lagged 1 period	Louisiana Department of Wildlife and Fisheries
TEMPSIX	Temperature associated with early juvenile shrimp abundance measured in degrees Celsius (°C)	Louisiana Department of Wildlife and Fisheries
SALISIX	Salinity associated with early juvenile sampling measured in part-per-thousand	Louisiana Department of Wildlife and Fisheries
RATEC	River flow rate at Tarbert landing (Mississippi) and Simmersport (Louisiana) measured in 1000 m ³ per 24 h period	Louisiana Department of Wildlife and Fisheries
FGR	Turbulent and stormy weather condition associated with cold front approaching Louisiana and winds typically blowing southwest	Muller and Willis (1983), Childers et al. (1990), Haas et al. (2001)
GR	Flow of warm, moist maritime air blowing from the Caribbean to Gulf and Louisiana	Muller and Willis (1983), Childers et al. (1990), Haas et al. (2001)
TURBSIX	Water clarity associated with early juvenile abundance measured as Secchi depth recorded in feet and tenths	Louisiana Department of Wildlife and Fisheries
NUMSXN (late juvenile)	Number of shrimp per 10 min 4.8 m otter trawl with 19.05 mm mesh size	Louisiana Department of Wildlife and Fisheries
NUMSXN _t	NUMSXN lagged <i>t</i> periods (<i>t</i> =0–5)	Louisiana Department of Wildlife and Fisheries
TEMPSXN	Temperature associated with late juveniles abundance and measured in degrees Celsius (°C)	Louisiana Department of Wildlife and Fisheries
SALISXN	Salinity associated with early juvenile sampling measured in part-per-thousand	Louisiana Department of Wildlife and Fisheries
TURBSXN	Water clarity associated with late juvenile abundance and measured as Secchi depth recorded in feet and depth	Louisiana Department of Wildlife and Fisheries
EFFORT	Nominal effort which is the relative fishing power of each vessel in the Gulf of Mexico shrimp fleet relative to a standard vessel	Dr. Wade Griffin, Texas A&M University
EFFORT ₁	EFFORT lagged 1 period.	Dr. Wade Griffin, Texas A&M University
CPUE	Index of relative abundance estimated as monthly reported white shrimp catch standardized by real effort	Estimated
CATCH	Monthly reported white shrimp catch	U.S. National Marine Fisheries Service

Effort was expressed in 24 h of tow time (i.e., 1 day is equal to 24 h of tow time) and the nominal fishing effort collected by NMFS was adjusted for variations in fishing power among different vessels as well as changes in fishing power over time (Griffin et al., 1997). Hence, the estimate of adult abundance is equivalent to catch per day where a day fished is standardized for heterogeneity of the fleet over time.

LDWF also provided mean monthly Mississippi River Flow (at Tarbert Landing, Mississippi) and Atchafalaya River flow (at Simmesport, Louisiana) measurements for use in this study. All flows were measured in thousand of cubic feet per second in a 24 h period. Turbidity measures used in the analysis were reported as secchi disk depth in feet at each shrimp sampling site, while salinity was recorded in parts-per-thousand (ppt) using a salinometer. Finally, no information is routinely collected pertaining to accumulated wetland loss (LANDLOSS). Estimates used in the study are derived from Turner (1997) and were provided by the author. Wetland loss estimates were annual in nature and were not converted to monthly values. Thus, while the estimate of accumulated wetland loss is permitted to increase from 1 year to the next in this study, it remains constant for all 12 months within any given year. Accumulated wetland loss is expressed in square kilometers per year and, because it is cumulative, increases over time.

2.5. Statistical methods

The model consisted of three interrelated equations depicting different life stages of Louisiana white shrimp. The explanatory variables are listed on Table 2 with their definition, measurement units and sources. The first equation for the early juvenile stage was specified as:

$$\begin{aligned} \text{NUMSIX}_t = & \alpha_0 + \alpha_1 \times \text{TEMPSIX}_t + \alpha_2 \times \text{SALISIX}_t \\ & + \alpha_3 \times \text{TURBSIX}_t + \alpha_4 \times \text{RATEC}_t \\ & + \alpha_5 \times \text{LANDLOSS}_t + \alpha_6 \times \text{GR}_t \\ & + \alpha_7 \times \text{FGR}_t + \varepsilon_{t1} \end{aligned} \quad (1)$$

where the term (*t*) reflects the current period.

The exogenous variables included in the early juvenile equation represent those factors which were expected to influence estimated abundance and for which data were available. A review of the literature suggested the hypotheses that white shrimp production were positively related to temperature (Turner, 1979) and negatively related to salinity and river flow (see, for example, Turner, 1979; Barrett and Gillespie, 1973), even though these relationships have not been shown to significantly influence penaeid early life stages. The expected

relationship between turbidity and early juvenile abundance was uncertain, as increased clarity might increase predation (negative effect) and/or the primary production that serves as food resources (positive effect). In addition, water clarity may impact the catchability of early juveniles via visual escapement mechanisms (Haas et al., 2001). The hypothesized relationship between early juvenile white shrimp abundance and accumulated wetland loss was assumed negative because Louisiana wetlands provide critical habitat during the early-life stages of shrimp (Turner, 1997; Pauly and Ingles, 1988). Specifically, wetland loss was anticipated to result in a monotonic decline in shrimp abundance at the early-life stages. Lastly, the expected relationships between early juvenile abundance and the measures of GR and FGR were unknown.

The second equation, that depicting late juvenile abundance, was specified as:

$$\begin{aligned} \text{NUMSXN}_t = & \beta_0 + \beta_1 \times \text{NUMSIX}_t \\ & + \beta_2 \times \text{NUMSIX}_{t-1} + \beta_3 \times \text{TEMPSXN}_t \\ & + \beta_4 \times \text{SALISXN}_t + \beta_5 \times \text{TURBSXN}_t \\ & + \beta_6 \times \text{RATEC}_t + \beta_7 \times \text{LANDLOSS}_t \\ & + \beta_8 \times \text{GR}_t + \beta_9 \times \text{FGR}_t + \varepsilon_{t2} \end{aligned} \quad (2)$$

where NUMSIX_{t-1} represented the estimated abundance of early juveniles lagged one period (month). Given the fast growth rate of early juvenile shrimp, a lag of more than one period was considered unwarranted (Garcia, 1985; Jones et al., 1970; Rothlisberg, 1982; Shanks, 1987; Baxter and al., 1988). Late juvenile abundance was hypothesized to be positively related to current and lagged early juvenile abundance.

The final equation of the model described adult abundance and was specified as:

$$\begin{aligned} \text{CPUE}_t = & \gamma_0 + \gamma_1 \times \text{NUMSXN}_t + \gamma_2 \times \text{NUMSXN}_{t-1} \\ & + \gamma_3 \times \text{NUMSXN}_{t-2} + \gamma_4 \times \text{NUMSXN}_{t-3} \\ & + \gamma_5 \times \text{NUMSXN}_{t-4} + \gamma_6 \times \text{NUMSXN}_{t-5} \\ & + \gamma_7 \times D_t + \gamma_8 \times \text{RATEC}_t + \gamma_9 \times \text{GR}_t \\ & + \gamma_{10} \times \text{FGR}_t + \gamma_{11} \times \text{EFFORT}_t + \gamma_{12} \\ & \times \text{EFFORT}_{t-1} + \gamma_{13} \times \text{TEMPSXN}_t + \varepsilon_{t3} \end{aligned} \quad (3)$$

The endogenous variable, $\text{CPUE}(t)$, was used as a proxy for an index of relative adult abundance and is estimated as monthly industry reported white shrimp catch in Louisiana standardized by effort. For purposes of analysis, CPUE was estimated in terms of both numbers of shrimp and kilograms. With respect to numbers, shrimp landings recorded in count/size categories were used for an estimate of fishery numbers to be extracted from kilograms data. This allowed a direct comparison of numbers in and numbers out of each age class, thus eliminating a significant portion of confounding effects from individual growth. As discussed in a subsequent section of the paper, however, estimation of Eq. (3) with CPUE expressed on the basis of kilograms, in conjunction with the estimation with CPUE expressed in numbers, allows for the examination of the change in individual

growth rate (independent of number of shrimp) associated with a change in any exogenous variable.

The large number of lagged late juvenile abundance variables in the adult abundance equation reflected the fact that shrimp, while essentially an annual crop, can live for a number of months upon entering the Gulf. The 5-month lag associated with late juveniles, in association with the 2-month period (this includes current month) associated with movement of early juveniles to late juveniles, suggested that environmental factors occurring as much as 6 months previous could impact adult abundance. This period is thought to cover the vast majority of an adult shrimp's life, and we hypothesized a positive relationship between current and lagged late juveniles and adult abundance. An unrestricted lag model was deemed inappropriate due to the presence of multicollinearity in the exogenous variables. Hence, a distributed lag model was tested and imposed on the system. The analysis suggested that the lag structure was one of geometric decay and that the appropriate lag length was six periods (current late juveniles and a 5-month lag of late juveniles).

One of the management tools employed by the LDWF is seasonal closures of inshore waters. With respect to white shrimp, the inshore waters are opened in August and remain open throughout the remainder of the calendar year (inshore waters are closed to brown shrimp harvesting activities when early life stages of white shrimp begin showing up in significant numbers). To capture the effects of closures, the discrete variable D_t was incorporated into the adult abundance equation and set equal to zero for the months January through July and to one for the months August through December. While the opening of inshore waters for white shrimp harvesting does not directly impact adult abundance (it could indirectly influence it through fishing mortality), failure to account for the time period when inshore waters are open could result in significant model misspecification.

The variable EFFORT_t was used to account for the amount of real shrimp effort exerted in the white shrimp fishery. Given the relatively fixed stock in any given month, increases in effort should result in declining abundance and, as such, the hypothesis of a negative relationship between effort and CPUE. Effort lagged one period was also included in an attempt to capture the impacts of past fishing pressure on current abundance, where the relationship between the two was expected to be negative.

There are a number of statistical considerations that influence the interpretation of the above model specifications. First, while the current level of any given environmental variable was anticipated to directly impact the different life stages of white shrimp abundance, previous levels of the environmental factors might also directly influence abundance. Thus, a 2-month moving average was used in the construction of all environmental variables in all equations. For example, river flow rates in July, denoted $\text{RATEC}(7)$, actually reflect a simple 2-month moving average of river flow rates (i.e., June and July average). A second consideration concerns the functional form used in estimating the equations. In general, theory provides little guidance regarding the functional relationship between the endogenous and exogenous variables in abundance equations. Preliminary analysis of the data using a Box-Cox transformation procedure (see Pindyck and Rubinfeld, 1991) suggested that a double-log model might

best represent the relationship, and this functional form was adopted for all model equations. Finally, the three abundance equations bear a close conceptual relationship with each other and, as such, one would expect correlation in the error terms across the different equations. To address this issue, Seemingly Unrelated Regression (SUR; Pindyck and Rubinfeld, 1991) was employed to increase the efficiency of the estimated parameters. Because a distributed lag model could not be estimated directly in an SUR framework, parameters associated with the current and lagged late juveniles were restricted in the SUR model to equal those determined from the first-stage ordinary least squares estimation.

3. Results

Selected statistics associated with the regression analysis are presented in Table 3 (kilograms of shrimp) and Table 4 (numbers of shrimp). Results show that most of the environmental variables significantly contribute to the prediction of abundance, expressed in either kilogram of shrimp or number. The predicted monthly adult abundance (CPUE), derived by iterative substitution of the parameters associated with Eqs. (1) and (2) into Eq. (3), along with the observed adult abundance are illustrated in Fig. 2. As indicated, the predicted adult abundance tends to “mirror” the observed adult abundance except in those rare instances where the observed values were abnormally low. The goodness of fit for the CPUE model using the root mean square error is 0.5175. The closer this value is to zero (as in this case), the better

Table 3
Results for the recursive three-equation model (index of abundance is in kilograms)

Label	Early juvenile (Numsix)	Late juvenile (Numsxn)	CPUE
Intercept	1.850	1.419	10.285*
TEMPSIX	4.998*		
SALISIX	0.066		
TURBSIX	0.124*		
RATEC	-0.686**	-0.044	-0.223*
LANDLOSS	-1.420*	-0.223*	
GR	-0.171	-0.020	0.008
FGR	-0.084	-0.003	0.006
NUMSIX		-0.010	
NUMSIX11		0.032*	
TEMPSXN		0.754*	-0.586*
SALISXN		0.383**	
TURBSXN		0.659*	
NUMSXN1			0.115*
NUMSXN11			0.094*
NUMSXN12			0.072*
NUMSXN13			0.051*
NUMSXN14			0.030**
NUMSXN15			0.008
D			0.931*
EFFORT			-0.293*
EFFORT1			0.006

Most of the reported parameters are significant at the 5% alpha level. System R^2 is 0.551.

* Significant at the 5% alpha level.
** Significant at the 10% alpha level.

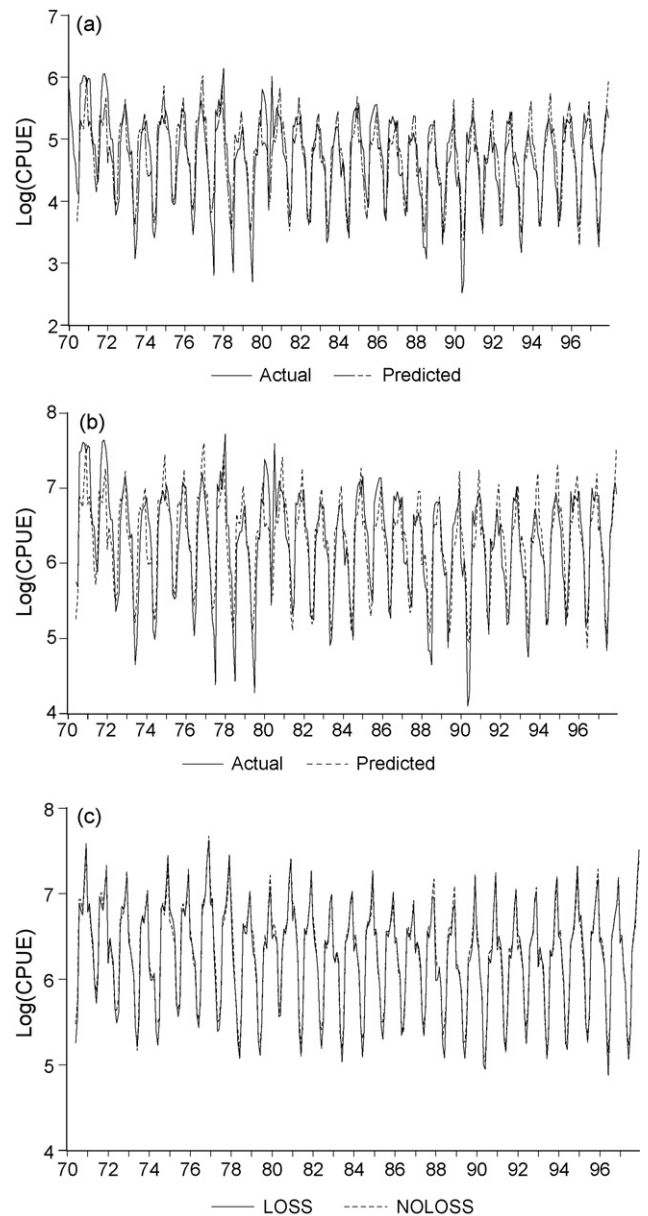


Fig. 2. (a) Actual and predicted catch per unit of effort (CPUE) expressed in numbers 1970–1997. (b) Actual and predicted catch per unit of effort (CPUE) expressed in kilograms 1970–1997. (c) Simulated log of catch per unit of effort (CPUE) with wetland loss held at the rate of 1970 and wetland loss held at its historical values.

the model simulates the actual data. We tested for autocorrelation in the three equations and results rejected the presence for autocorrelation in the first two equations. We could not reject the presence of autocorrelation in the adult abundance equation. Therefore we corrected the adult abundance equation for first order serial correlation using the Hildreth–Lu approach (1960). As suggested by an anonymous reviewer, we excluded all the non-significant factors from the analysis. Since, the sizes of the estimated coefficients did not change significantly we are, therefore, presenting and discussing only the results of the full model hereafter.

As expected, the positive relationship between temperature (TEMPSIX) and early juveniles is evidence that warmer tem-

peratures are conducive to growth, to decreasing the duration of the more vulnerable early life stages and, therefore, the early juvenile white shrimp survival and abundance (Tables 3 and 4). The elasticity, which indicates a percent change in a dependent variable due to a percent change in an independent variable, is about five for early juveniles indicating that a 1% change in temperature is associate with a 5% change in early juvenile abundance (Tables 5 and 6). The effects of temperature appear to decrease as shrimp grow and move offshore. For instance, when adult abundance is expressed in terms of numbers, a 1% change in temperature in the upper marshes (TEMPSIX) was found to result in a very moderate increase in adult abundance, 0.05. While marginally higher when expressed in pounds (0.057), the influence of this factor, which is highly influential on an early life stage, is substantially eroded by the time the shrimp reaches a harvestable size.

A positive relationship was also found between temperature around those stations sampled with the 4.8 m otter trawls (TEMPSXN) and late juvenile abundance, expressed in either kilograms of shrimp (Table 3) or numbers (Table 4). Somewhat unexpectedly, however, an increase in this temperature was found to result in lower adult abundance. This may reflect increased susceptibility to predation as shrimp grow and begin their emigration from the more protected marsh areas to open waters.

Survival of juvenile shrimp associated with various degrees of salinities is well documented in the literature (Bray et al., 1994; Kumulu and Jones, 1995; Rosas et al., 1999; Tsuzuki et

Table 4
Results for the recursive three-equation model (index of abundance is in numbers)

Label	Early juvenile (Numsix)	Late juvenile (Numsxn)	CPUE
Intercept	2.068	1.337	15.41*
TEMPSIX	4.998*		
SALISIX	0.090		
TURBSIX	0.126*		
RATEC	-0.671**	-0.058	-0.204*
LANDLOSS	-1.422*	-0.188*	
GR	-0.169	-0.021	0.008
FGR	-0.087	-0.001	0.018
NUMSIX		-0.010	
NUMSIX11		0.013*	
TEMPSXN		0.201*	-1.275*
SALISXN		0.206**	
TURBSXN		0.209*	
NUMSXN1			0.115*
NUMSXN11			0.129*
NUMSXN12			0.102*
NUMSXN13			0.076*
NUMSXN14			0.049**
NUMSXN15			0.023
D			1.515*
EFFORT			-0.340*
EFFORT1			-0.028

Most of the reported parameters are significant at the 5% alpha level. System R^2 is 0.589.

* Significant at the 5% alpha level.

** Significant at the 10% alpha level.

Table 5
Derived elasticities with respect to various environmental factors and effort

Label	Early juvenile (Numsix)	Late juvenile (Numsxn)	CPUE
Intercept			
TEMPSIX	4.998	0.753	0.045
SALISIX	0.066	0.003	0.011
TURBSIX	0.124	0.383	0.003
RATEC	-0.689	-0.084	-0.255
LANDLOSS	-1.420	-0.228	-0.092
GR	-0.171	-0.003	
FGR	-0.085	-0.024	
TEMPSXN		0.730	0.118
SALISXN		0.348	0.139
TURBSXN		0.648	0.259
EFFORT			-0.293

An elasticity is for example a percentage change in early juvenile abundance with respect to a percentage change in temperature (CPUE in numbers rather than kilograms).

al., 2000; Saoud and Davis, 2003). Our results also indicated a positive relationship between water salinity levels and white shrimp abundance, with a 10% increase in salinity (SALISIX) leading to a 0.66% increase in the number of early juveniles, a 0.03% increase in the number of late juveniles, and a 0.001 increase in the catch expressed in numbers (Table 5). A larger impact is observed at the stations where 4.8 m otter trawls are used for sampling. Specifically, a 10% increase in salinity levels associated with late juveniles (SALISXN) was estimated to result in about a 3.58% increase in the number of late juveniles and a 1.4% increase in the proxy for adult abundance, i.e., CPUE (Table 5).

In general, the effects of water salinities on white shrimp abundance were found to be larger when examined on the basis of kilograms rather than when examined on the basis of numbers. For example, a 10% increase in salinity levels associated with early juveniles (SALISIX) was found to result in a 0.90% increase in adult abundance expressed in kilograms (Table 6), or almost one and half the estimated 0.66% increase when estimated on the basis of numbers (Table 5). Similarly, adult

Table 6
Derived elasticities with respect to various environmental factors and effort

Label	Early juvenile (Numsix)	Late juvenile (Numsxn)	CPUE
Intercept			
TEMPSIX	4.993	0.107	0.057
SALISIX	0.090	0.002	0.001
TURBSIX	0.126	0.003	0.001
RATEC	-0.671	-0.072	-0.243
LANDLOSS	-1.472	-0.219	-0.117
GR	-0.170	-0.024	-0.004
FGR	-0.087	-0.003	0.016
TEMPSXN		0.746	-0.876
SALISXN		0.358	0.191
TURBSXN		0.667	0.356
EFFORT			-0.221

An elasticity is for example a percentage change in early juvenile abundance with respect to a percentage change in temperature (CPUE in kilograms rather than numbers).

abundance, expressed in pounds, was found to increase by 1.9% as a result of a 10% increase in salinity levels associated with late juveniles (SALISXN) compared with the 1.4% increase when examined on the basis of numbers of shrimp. As discussed in more detail below, this differential reflects the individual growth rate of shrimp.

Though salinity was found to positively influence adult abundance, holding other factors constant, river flow rate (RATEC) was found to negatively influence adult abundance. The effect, furthermore, is relatively large with a 10% increase in the rate resulting in an estimated 2.4% decline in adult abundance.

Turbidity in the estimated model was associated with increasing white shrimp abundance. The effect was more pronounced with late juveniles sampled with a 4.8 m otter trawl (TURB-SXN). For example, a 10% increase in turbidity around those stations was associated with a 6.67% increase in the number of late juvenile shrimp and a 3.56% increase in harvested shrimp (Table 5). Expressed in pounds, a 10% increase in turbidity around the stations where 4.8 m otter trawl are used for sampling was found to result in a 2.59% increase in adult abundance (Table 6).

The estimated model also indicated that the loss of wetlands has a negative impact on the abundance of early juvenile white shrimp. For example, a 1% increase in cumulative wetland loss was related to a 1.42% decrease in the number of shrimp at the early stage of life, holding other factors constant. While this negative effect lessens as the shrimp progresses through its life stages (-0.219% for late juveniles and -0.117 for adults), the cumulative impact in loss in abundance has serious implications for commercial catch. These estimated impacts are illustrated in Fig. 2. The curve labeled ‘no loss’ reflects estimated adult abundance (CPUE) under the base scenario. This scenario is portrayed using actual values for all exogenous variables during the period of analysis with the exception of cumulative wetland loss, which is set at the observed 1970 value throughout the 28-year simulation period. The curve labeled ‘cumulative loss’ reflects the estimated adult abundance (CPUE) allowing cumulative wetland loss to increase over the 1970–1997 period. As indicated, the differential between expected catch under the ‘no loss’ scenario and expected catch under the ‘cumulative loss’ scenario increases over the period of analysis and by 1997 is equal to about 7.5%. Given current estimates of future wetland losses under the assumption of only limited coastal restoration activities (estimated to be about 25 square miles per year) one can anticipate continued declines in all life stages of white shrimp.

The pressure exerted by the fishing fleet on the total shrimp stock has the potential for decreasing the catch per unit of effort (CPUE). Results showed that a 10% increase in fishing effort leads to a 3% decrease (2.93 exactly) in CPUE (Table 6). Shrimp effort throughout the Gulf of Mexico has fallen sharply since the mid-1980s which helps to explain the relative long-run stability in CPUE despite an increasing cumulative wetland loss. However, as indicated by one anonymous reviewer, one caveat in the analysis is that γ_{12} coefficient in Eq. (3) ($CPUE = \gamma_{12} \times EFFORT_{t-1}$) is simply catch, and catch removals explain the short term decrease in CPUE. Over the long term (i.e., equilibrium conditions) CPUE has a negative relation-

ship to effort in which the slope is $-k/r$, but that does not apply to non-equilibrium observations. Therefore, the conclusion that “a 10% increase in fishing effort leads to a 3% decrease in CPUE” is conditional on equilibrium conditions and has all the same problems (i.e., overestimation of productivity) as the early biomass dynamics models that assumed equilibrium conditions.

A pound of shrimp is equal to the number of shrimp multiplied by the average weight per shrimp expressed as a fraction of kilogramms (e.g., 1/100th of a pound for 100 count shrimp). The difference between the estimated elasticities associated with adult abundance expressed in kilograms (Table 6) and the estimated elasticities associated with adult abundance expressed in numbers (Table 5) thus provides an estimate of the elasticity of growth, expressed on a weight basis. Thus, for example, a 10% increase in salinity levels associated with late juveniles (SALISXN) results in about a one-half of 1% (0.49) increase in individual growth rate at the adult stage. Similarly, a 10% increase in turbidity levels associated with late juveniles (TURB-SXN) culminates in a 1.1% increase in the individual growth rate at the adult stage. Conversely, however, increases in accumulated wetland loss are found to result in lower growth rates with a 10% increase in the former leading to about a 0.2% increase in the later.

4. Discussion

The goal of this study was to develop a predictive model for white shrimp abundance based on environmental and biological factors using a recursive three-equation model. This strategy allowed the examination of the full impacts of environment or biological shocks on various life stages. Overall results positively linked temperature and salinity with abundance of shrimp at its early life stages. Wetland loss over time and higher river discharge decreased the abundance of shrimp, while biological factors such as the higher abundance of early juveniles predicted well the late juveniles, with a similar relationship existing between the late juveniles and adult CPUE.

The analysis indicated, however, that the influence of many environmental factors that significantly impact the number of white shrimp in their early life stages is largely eroded by the time the shrimp reach an adult stage. This finding, while not unexpected given the high instantaneous mortality rate of shrimp, does suggest that attempts to accurately predict adult abundance based on one or more environmental factors encountered by the shrimp at earlier life stages will continue to challenge researchers and, more importantly, fishery managers.

As with any analysis, the results obtained in this study were dependent on the assumptions employed in model development and the data used. Two assumptions used in the current model that warrant additional consideration relate to the 2-month moving average associated with creation of all environmental data and the length of the lags used in the analysis (particularly the impact of late juveniles on adult abundance). While the overall results appear to be relatively robust to small changes in the time frame used in the moving average process and the lag length, some parameters were indeed sensitive and additional research is warranted. Finally, as with any model, results are only as accu-

rate as the data used. The wetland loss data used in this paper, as noted, came from analysis by Turner (1997). His analysis provided a hypothesis regarding wetland loss and the data is based on this hypothesis. To the extent that the hypothesis may not be valid, the wetland loss data used in this paper and subsequent estimated parameters associated with wetland loss may be somewhat biased.

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