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ASPECTS OF BROWN SHRIMP, *PENAEUS AZTECUS*, GROWTH IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

The growth of brown shrimp, *Penaeus aztecus*, was studied by utilizing forms of growth models compatible with mark-recapture data. The analysis of 5,100 individuals marked and later recaptured in the northern Gulf of Mexico indicates that the von Bertalanffy model is slightly superior to the logistic in reflecting growth in length and the monomolecular model is superior to the Gompertz in expressing growth in weight. Linear functions are apparently inadequate growth models for brown shrimp. Estimated size-age relationships are appreciably different for each sex in that females are much larger than males of the same age. The pattern of growth shown in this analysis for populations in the northern Gulf is different from that reported in the southern Gulf off the Mexican coast and that reported in U.S. Atlantic coastal waters.

The commercial importance of brown shrimp, *Penaeus aztecus* (Ives 1891), has precipitated several studies of the growth rate for individuals of that species. Definition of the growth rate is necessary in order to develop an understanding of the population dynamics of the resource. Growth models have been reported for wild populations in the northwest Atlantic off North Carolina (McCoy 1972) and in the southern Gulf of Mexico off Tampico, Mexico (Chávez 1973). Several workers have described the growth rate of small brown shrimp in the northern gulf (George 1962; St. Amant et al. 1963, 1966; Loesch 1965; Ringo 1965; Jacob 1971; Wengert 1972; Gaidry and White 1973; Rose et al. 1975; Welker et al. 1975; Knudsen et al. 1977). The growth rate of larger brown shrimp, however, has not been documented for populations in the northern gulf.

Generally, growth equations define the relation between the size and age of individual animals. Three such equations descriptive of growth are the logistic (Pearl and Reed 1920), von Bertalanffy (Bertalanffy 1938), and Gompertz (Gompertz 1825; Silliman 1967) functions. The logistic and von Bertalanffy models are employed to reflect growth in length whereas the Gompertz is usually used to model growth in weight. The von Bertalanffy function may be directly fit to weight data to model growth in weight. If it is so used, it is then correctly referred to as the monomolecular growth model (Medawar 1945; Fabens 1965). This study appraised the abilities of these functions to model brown shrimp growth. Additionally the linear relation between size and age was also considered.

The absolute age of shrimp cannot be determined directly by counting annuli on hard parts. Shrimp molt many times during their life cycle; all hard parts are lost, then reformed with each molt. Therefore, age-size data of individuals cannot be obtained for growth modeling; another technique must be employed. Although the age of brown shrimp at mean size has been discerned from large volume size-frequency samples (Chávez 1973), age was not directly observable and therefore was inferred. Mark-recapture data affords a direct measure of the changes in size per change in time. Forms of the growth functions were employed to utilize mark-recapture data so that error resulting from incorrect age determination was avoided.

METHODS

Brown shrimp spawn in offshore Gulf of Mexico waters (14-100 m deep) throughout the year (Cook and Lindner 1970). Eggs hatch within 14-18 h (Cook and Murphy 1966) and larvae undergo metamorphosis within 12-15 days (Cook and Lindner 1970). Shrimp then migrate into estuaries to undergo their juvenile period. Large juvenile shrimp, usually 75-90 mm total length, migrate to offshore waters as they become sexually mature, thus completing the life cycle. Ap-

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proximately 80% of the recaptured individuals utilized in this analysis were large juveniles when marked. These shrimp were marked and released in estuarine waters before migrating to offshore waters (Table 1). The remaining 20% were large adults marked and released in offshore gulf waters along the Texas coast. These marking experiments were carried out during 1967, 1968, and 1969. A full explanation of the data is given by Clark et al. (1974). These data include total length (i.e., the distance from the anterior end of the rostrum to the posterior end of the telson) when released and when recaptured, the dates of release and recapture, and the sex of each individual. Data entries with the same release and recapture dates do not reflect growth and therefore were not used to estimate growth rates.

In order to analyze growth in weight, release and recapture length were converted to weights according to weight-length relations. These relations were estimated from data collected from the commercial landings at Galveston, Tex., during June, September, and December of 1965 and March of 1966 (Fontaine and Neal 1971). Parameters of the model weight $= a$ (length)^b were estimated for males and for females separately by minimizing the expression $\sum^{n} (W - W_o)^2$ where W is weight defined by the model, W_o is observed weight, and n is the number of observations. The Marquardt algorithm (Marquardt 1963) was employed to find the minimum. Plots of the estimated relations through the scatter of the observations were observed to discern male/female differences and the predictive usefulness of the models.

Since mark-recapture data were employed, growth functions of interest were expressed in terms of the change in age rather than absolute age (see Appendix for derivation of equations). Each recaptured individual was of some unknown age on the date marked and on the date recaptured so that the change in age is equivalent to the time at large. Expressed in these terms the logistic function changes from

$$S_a = S_\infty/(1 + be^{-ka}) \tag{1a}$$

to

$$S_r = S_\infty/(1 + [(e^{-k(\triangle a)})\ (S_\infty - S_m)/S_m]) \tag{1b}$$

by substitution and rearrangement of terms. Likewise, the von Bertalanffy equation

$$S_a = S_\infty(1 - be^{-ka}) \tag{2a}$$

is expressed as

$$S_r = S_\infty - (S_\infty - S_m)e^{-k(\triangle a)}. \tag{2b}$$

The Gompertz function

$$S_a = S_i \exp[G(1 - \exp[-g(a - a_i)])] \tag{3a}$$

becomes

$$S_r = S_i[\exp G][S_m/(S_i \exp G)]^{\exp[-g(\triangle a)]}. \tag{3b}$$

A linear function of size upon age

$$S_a = b + ka \tag{4a}$$

is written

$$S_r = S_m + k\,(\triangle a)\,. \tag{4b}$$

Definitions of symbols employed above are:

S_a = size at age a,
S_r = size at recapture,
S_m = size when marked,
S_i = size of the smallest animal in the data,
a_i = age of the smallest animal in the data,

TABLE 1.—Brown shrimp mark-recapture experiments, northern Gulf of Mexico.

Release area	Release date	Length range (mm) of released shrimp	Length range (mm) of recovered shrimp	Number recovered
Galveston Estuary	May 1967	66-175	71-124	13
50 mi east of Galveston, Tex.	June 1967	83-147	86-178	301
60 mi southeast of Freeport, Tex.	Sept. 1967	122-181	124-196	40
Biloxi Bay, Miss.	May 1968	90-122	90-181	4,218
40 mi southeast of Freeport, Tex.	Feb.-Mar. 1969	109-168	136-185	69
Galveston Estuary	June-July 1969	90-128	91-182	257
50 mi southeast of Freeport, Tex.	Nov. 1969	145-203	141-213	593

S_∞ = an equation parameter, the asymptotic size,
b = an equation constant related to the size at birth,
$\Delta a = a_r - a_m$ = time at large,
a_r = age of an individual on the date recaptured,
a_m = age on the date marked and released,

and G, g, and k are equation parameters.

Equation parameters S_∞, k, G, and g were estimated by utilizing the Marquardt algorithm to minimize the residual sum of squares:

$$\sum^{n} (S_r' - S_r)^2$$

where n = the number of individuals marked and recaptured,
S_r' = the observed size at recapture, and
S_r = the size at recapture as estimated by the growth equation.

The remaining equation constants, b in Equations (1a) and (2a) and a_i in Equation (3a), are respectively computed:

$$b = (S_\infty / S_b) - 1 \qquad (5a)$$

$$b = (S_\infty - S_b)/S \qquad (5b)$$

$$a_i = \ln\left[1 - \frac{\ln(S_b/S_i)}{G}\right]g \qquad (5c)$$

where S_b is the size at birth and other symbols are as before. The parameter b in Equation (4a) is simply the size at birth.

Studies of the early development of brown shrimp indicate that newly hatched larvae are 0.35 mm total length (Cook and Murphy 1971). Estimates of the equation constant b in the logistic and von Bertalanffy models were based on that length at birth.

Shrimp eggs are 0.26 mm in diameter (Cook and Murphy 1971) and about the density of water (Cook and Lindner 1970) so that the weight at hatching is about 0.000009 g. Brown shrimp undergo metamorphosis 11 to 15 days after hatching (Cook and Lindner 1970) and are 0.0008 g at that time (Wheeler 1969). The weight at birth was calculated as the midpoint between that weight and the egg weight. Calculations of b and a_i in the various models were based on that weight at birth.

RESULTS

Growth in Length

In anticipation that differences in growth between sexes may exist, equations were fit for males and females separately. Estimated equation parameters (Table 2) are quite different between sexes. The fitted models indicate that females are much larger than males of the same age. The estimates of the growth coefficient k do not differ greatly between sexes for both the logistic and the von Bertalanffy models; the 90% probability support plane confidence intervals (Conway et al. 1970) extensively overlap for both models. The estimates of asymptotic length are, however, greatly different and such confidence intervals on those estimates are very disjoint. Pooling all data together to estimate overall growth functions for both sexes combined was therefore judged unrealistic.

The relative abilities of the von Bertalanffy, logistic, and linear models to correctly reflect growth was judged by comparing residual sums of squares (Table 3). The von Bertalanffy function produced the smallest residual and the linear model the largest. The residual sum of squares for the linear model was well over three times that of the von Bertalanffy and logistic models for both males and females. The difference between the two nonlinear models was much smaller; the residual of the logistic was but 8% larger than that of

TABLE 2.—Growth models for brown shrimp. Lengths (L) in millimeters, weights (W) in grams, and ages (a) in months.

Model	Males	Females
Logistic	$L = 162.8/(1 + 464.1429e^{-0.5664a})$	$L = 187.5/(1 + 534.7143e^{-0.6116a})$
von Bertalanffy	$L = 168.7(1 - 0.9979e^{-0.3357a})$	$L = 193.6(1 - 0.9982e^{-0.3363a})$
Linear	$L = 0.35 + 4.2181a$	$L = 0.35 + 7.8209a$
Gompertz	$W = 5.07(\exp[1.9996(1 - \exp[-0.3735(a - 4.6688)])])$	$W = 3.55(\exp[2.8359(2 - \exp[-0.4410(a - 3.2549)])])$
Monomolecular	$W = 43.51(1 - 0.9999e^{-0.1546a})$	$W = 74.32(1 - 0.9999e^{-0.1416a})$
Linear	$W = 0.0004045 + 1.8018a$	$W = 0.0004054 + 3.901a$

the von Bertalanffy in the case of males and 5% larger for females.

TABLE 3.—Residual sums of squares for six brown shrimp growth models.

Model	Males	Females
Length:		
Von Bertalanffy	44,161.65	155,797.40
Logistic	47,661.96	163,278.00
Linear	162,661.15	599,677.13
Weight:		
Monomolecular	5,548.57	33,930.69
Gompertz	7,027.72	38,751.26
Linear	12,335.42	67,526.07
Number of observations	1,536	3,588

The difference in growth between sexes and the ability of the von Bertalanffy model to fit the observations is visible from plots of the observed lengths about the growth models. Data points were plotted by first calculating the age at release from the fitted model, adding time at large to compute the age at recapture, then plotting that age and the recapture size. The plots (Figure 1A, B) show that sex specific growth does exist and that the differences are of significant magnitude. Further, the von Bertalanffy model does visibly fit the observed data. Although the observed data do

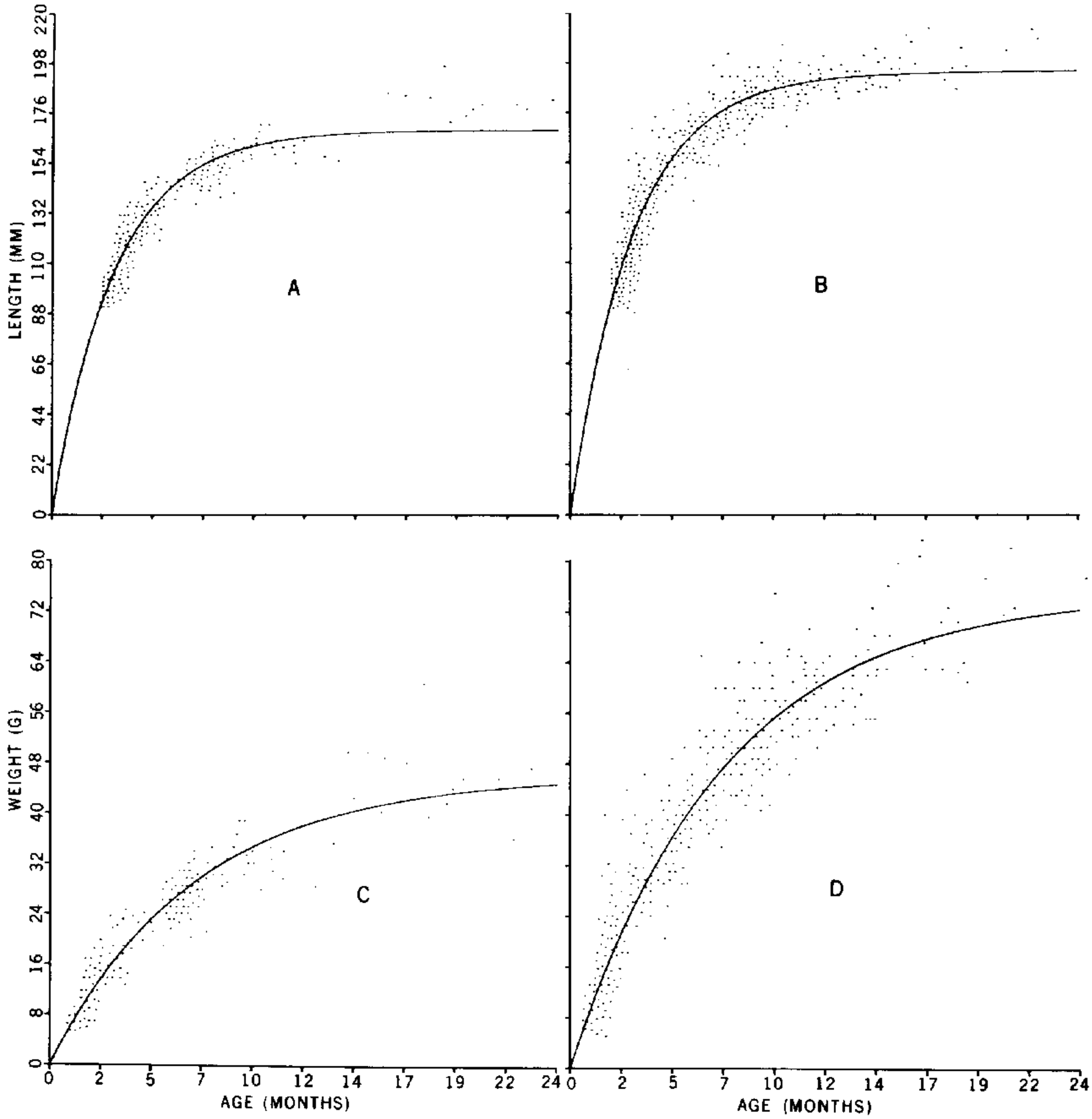

FIGURE 1.—Brown shrimp growth models. A) von Bertalanffy growth model, males; B) von Bertalanffy growth model, females; C) monomolecular model, males; D) monomolecular model, females.

not in general fall close to the modeled line, the scatter is not severe.

Growth in Weight

The Marquardt algorithm (Marquardt 1963) was employed to estimate parameters of weight-length relations used to transform individual release and recapture lengths into weights so that growth in weight could be modeled. Plots of the estimated relations (Figure 2) indicate them to be sex specific. Support plane confidence intervals (Conway et al. 1970) on equation parameters (90% probability) for males did not overlap those for females further indicating that the functions differ between sexes. In addition the data were logged to linearize the relation and covariance analysis techniques applied to test for differences between sexes. The probability that the linearized functions are the same is small ($P_r < 0.001$) further indicating the sex specificity of these relations. Further inspection of the plots shows the scatter of observations to be restricted and that the models effectively fit. These sex specific models were therefore employed to transform the data.

The magnitude of residual sums of squares (Table 3) indicates the monomolecular model is the best predictor of weight at age and the linear model the poorest. The residual term for the linear fit is about twice as large as that for the monomolecular model and about 1.8 times that of the Gompertz for both sexes. The reduction in residuals of the monomolecular model as compared with the Gompertz was much smaller, 25% in the case of males and 14% in the case of females.

As in the case of growth in length, estimated growth parameters indicate that growth in weight is sex dependent. Both the Gompertz and the monomolecular model estimate females to be much larger than males of the same age. Asymptotic weight (monomolecular model) is estimated to be 75 g for females and 46 g for males; support plane confidence intervals (90% probability) on these estimates do not overlap. Estimates of the parameter k in the monomolecular model appear to be about the same for both sexes and in fact the support plane confidence interval for males completely includes that interval for females.

The differences in growth between sexes and the degree of fit of the monomolecular model is shown in Figure 1. Although appreciable scatter is ap-

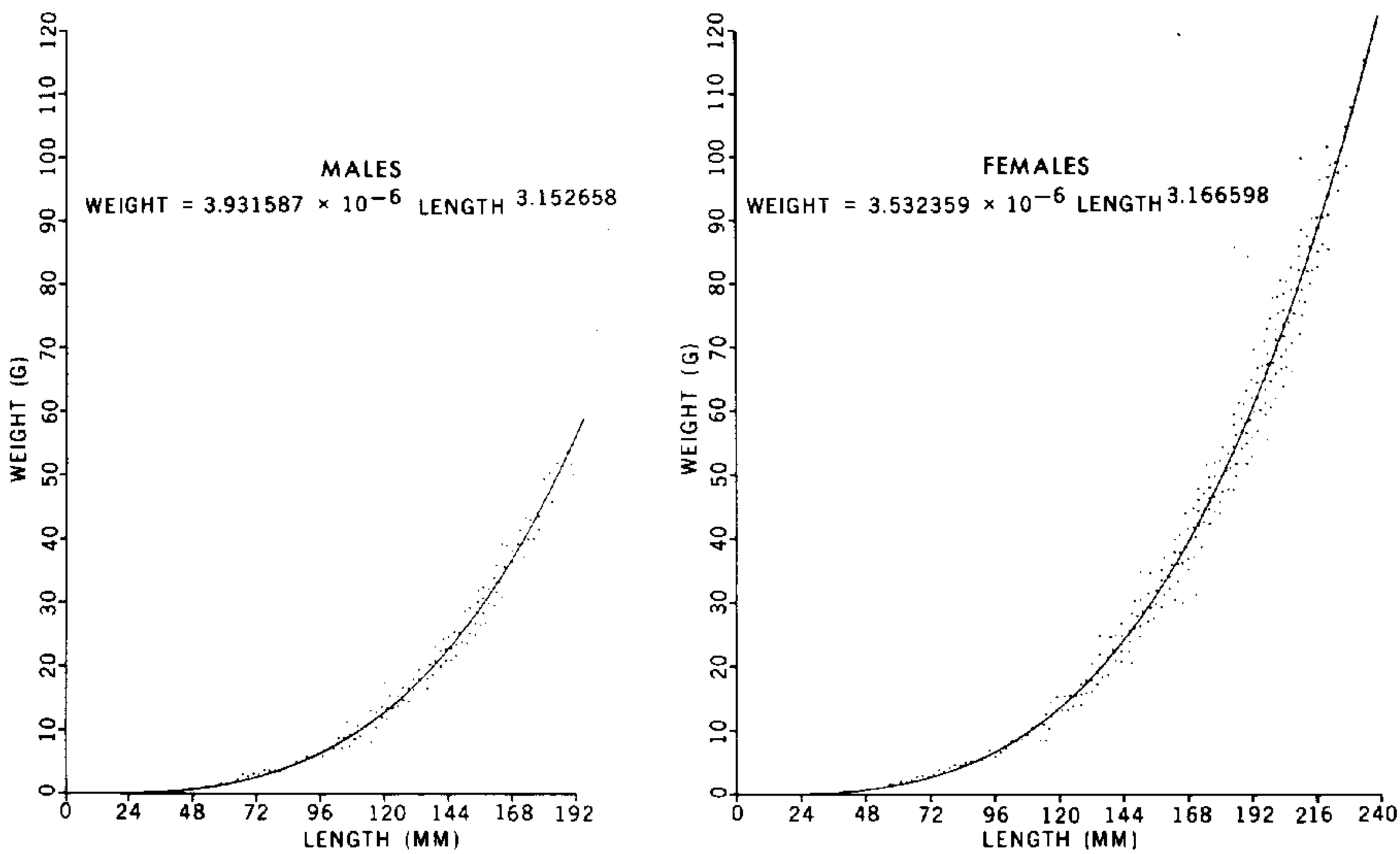

FIGURE 2.—Weight-length relationships for brown shrimp.

parent, systematic departure of the observed points from the model is not evident so that the model does reflect the data.

CONCLUSIONS

The relative abilities of prediction of the different models can be judged by comparison of their residual sum of squares. The comparison strongly suggests that the linear function was by far the poorest model of brown shrimp growth both in length and weight. Although the size-age relation does appear linear for small young individuals, the rate of increase in size decreases with age, a phenomenon documented for many organisms both terrestrial and aquatic. A nonlinear function is therefore required to model brown shrimp growth throughout their entire life span.

The residual sum of squares for the von Bertalanffy equation was smaller than the logistic equation when modeling weight; however, these differences were not large. It is therefore not completely evident that the von Bertalanffy equation is vastly superior to the logistic and Gompertz in the modeling of brown shrimp growth. The von Bertalanffy equation did, however, constantly fit these data best for both sexes in the modeling of both length and weight. This study does therefore show the von Bertalanffy model to be slightly superior to the logistic and the monomolecular model superior to the Gompertz for both sexes.

The difference in the size-age function between sexes was found to be large. This phenomenon was previously reported for brown shrimp in the southern Gulf of Mexico (Chávez 1973) and northwest Atlantic (McCoy 1972) and for many other marine organisms. This study indicates that male brown shrimp apparently grow to approximately only three-fifths the weight and five-sixths the length of females; however, the coefficients of growth, as indexed by k in the monomolecular and von Bertalanffy models, are roughly equivalent. It is interesting to note that the rate of increase in size tends to fall off at an earlier age for males than for females (see Figure 1). Since, in general, a decrease in that rate roughly conforms to the age of maturity and sexual activity, it is not unreasonable to assume that males mature at a younger age than do females.

Comparison of growth functions derived herein with those generated by other workers indicate that brown shrimp growth in the northern Gulf of Mexico is very different than that in the southern gulf and in U.S. Atlantic coastal waters. Growth functions derived from populations off Mexico (Chávez 1973) demonstrated a faster and prolonged growth compared with growth observed in this study. That trend was consistent for both males and females. Studies off North Carolina (McCoy 1972) showed growth in Atlantic waters to be very rapid although a smaller asymptotic size was realized. As before, that trend was the same for both sexes. The kinds of data used and the methods employed to fit the growth models differed in all three studies; therefore, some disagreement in results may be expected. The magnitude of the differences observed, however, indicated truly different rates of growth may well exist in the three geographical locations. The growth of wild populations of white shrimp, *Penaeus setiferus*, a similar species, is correlated with water temperature (Gaidry and White 1973) in the shallow estuarine and nearshore areas they inhabit throughout their entire life span. Since the temperature of seasonally homothermic deep offshore waters where brown shrimp spend their adult life may be assumed to increase with decreasing latitude, the differences in growth between northwest Atlantic, northern gulf, and southern gulf brown shrimp populations are likely positively correlated with gross water temperature.

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APPENDIX

The linear, logistic, and Gompertz functions were expressed in terms of size at release age, size at recapture age, and change in age (time at large) following the rationale presented by Fabens (1965) for the von Bertalanffy function (as follows).

Each individual was of some unknown age (a_m) upon the date marked (t_m) and released. Upon the recapture date (t_r) the individual was of an unknown older age (a_r) so that the difference between the release and recapture date (Δt) is equivalent to the increase in age (Δa) of that individual:

$$\triangle a = \triangle t = t_r - t_m = a_r - a_m \,. \tag{A1}$$

That equality can be substituted into the von Bertalanffy function when expressed in terms of the size at recapture (S_r) and the age at recapture. Therefore the von Bertalanffy equation

$$S_r = S_\infty [1 - b \exp(-ka_r)] \tag{A2}$$

becomes $S_r = S_\infty(1 - b \exp(-ka_m) \exp[-k(\triangle a)])$. (A3)

The equation, when expressed in terms of the size when marked (S_m) with rearrangement, is:

$$b \exp(-ka_m) = 1 - (S_m / S_\infty). \tag{A4}$$

That expression is substituted into Equation (A3) to yield the required function:

$$S_r = S_\infty - (S_\infty - S_m)\, e^{-k(\wedge a)}. \tag{A5}$$

That form can then be employed to estimate the equation parameters k and S from mark-recapture data. The final parameter (b) can be calculated directly by first rearranging terms of the original function:

$$S_a = S_\infty(1 - be^{-ka}) \tag{A6}$$

so that $b = [1 - (S_a / S_\infty)] / e^{-ka}$ (A7)

where S_a is the size at age a. If the size at birth, i.e., at age 0, is known, then:

$$b = 1 - (S_b / S_\infty) \tag{A8}$$

where S_∞ is estimated from Equation (A5) and the size at birth (S_b) is derived from life history studies.

That same rationale was applied to the logistic function. The size of a recaptured individual is expressed:

$$S_r = S_\infty / [1 + b \exp(-ka_r)] \,. \tag{A9}$$

Since $a_r = a + a_m$ substitution gives:

$$S_r = S_\infty / (1 + b \exp[-k(\triangle a)] b \exp(-ka_m)] \,. \tag{A10}$$

Expressing the logistic equation in terms of the size marked and rearrangement of terms gives:

$$b \exp(-ka_m) + [(S_\infty - S_m)/S_m] \,. \tag{A11}$$

Substitution yields:

$$S_r = S_\infty / [1 + ((e^{-k(\triangle a)})(S_\infty - S_m)/S_m)] . \quad \text{(A12)}$$

Since S_r, S_m, and Δa were all directly observable from mark-recapture data, the logistic equation parameters S_∞ and k may be estimated from the data set. The remaining equation constant was calculated by rearrangement of terms:

$$b = ((S_\infty/S_a) - 1)/e^{-k(a)} . \quad \text{(A13)}$$

From life history studies the size at birth, S_b, was determined. Since at birth age is zero ($a = 0$) the expression can be written:

$$b = (S_\infty/S_b) - 1. \quad \text{(A14)}$$

The Gompertz function was likewise expressed in terms of the mark-recapture data. From Equation (3a), the size at the time of marking is:

$$S_r = S_i \exp[G(1 - \exp[-g(a_r - a_i)])] \quad \text{(A15)}$$

and by substitution becomes

$$S_r = S_i \exp[G - G(\exp[-g(a_m - a_i)])(\exp[-g(\triangle a)])] . \quad \text{(A16)}$$

Writing in terms of the size at recapture and rearrangement of terms gives:

$$\exp(-G \exp[-g(a_m - a_i)]) = S_m/(S_i \exp G). \quad \text{(A17)}$$

Substitution yields the expression required to estimate the constants G and g from the mark-recapture data:

$$S_r = [S_i \exp(G)][S_m/(S_i \exp(G))]^{\exp[-g(\triangle a)]} \quad \text{(A18)}$$

where S_i was the smallest size observed in those data. The remaining equation constant, a_i, was then calculated by writing Equation (3a) in terms of the size at birth:

$$S_b = S_i \exp[G(1 - \exp[-g(a - a_i)])] . \quad \text{(A19)}$$

Since at birth age is zero ($a = 0$) the expression can be written as:

$$a_i = \ln(1 - [\ln(S_b/S_i)/G]/g) \quad \text{(A20)}$$

where S_b, the size at birth, was determined from natural history studies. The linear function:

$$S_a = b + ka \quad \text{(A21)}$$

requires a much simpler derivation. Expressed in terms of the size at recapture:

$$S_r = b + ka_r . \quad \text{(A22)}$$

Substitution gives:

$$S_r = b + k(\triangle a + a_m) . \quad \text{(A23)}$$

The function expressed in terms of the size at release

$$S_m = b + ka_m \tag{A24}$$

can be rearranged to

$$a_m = (S_m - b)/k \tag{A25}$$

which can be substituted into Equation (A23) to give

$$S_r = k \wedge a + S_m \ . \tag{A26}$$

The remaining parameter b is simply the ordinate intercept or the size at birth.