

Allometry of the Growth of Pink Shrimp *Farfantepenaeus duorarum* in a Subtropical Bay

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Abstract.—We developed robust allometric relationships for pink shrimp *Farfantepenaeus* (= *Penaeus*) *duorarum* by focusing on appropriate mathematical models and statistical procedures for parameter estimation. We utilized fishery-independent data on the abundance and size of juvenile and subadult pink shrimp from an efficient sampling program in Biscayne Bay, Florida. Total length (TL), carapace length (CL), and wet weight (W) were obtained from 440 male and 487 female pink shrimp ranging from 3 to 30 mm CL. The TL–CL function was linear. Because we noticed a pronounced shift in the relationship at the onset of sexual maturity, however, we estimated separate models for juveniles (CL < 18 mm; TL = 1.616 + 4.503·CL) and subadults (CL ≥ 18 mm; TL = 11.636 + 3.985·CL). The dependence of W on CL was best described by nonlinear allometric functions of the form $W = \alpha \text{CL}^\beta$. Model parameters were estimated by least-squares regression methods after log-transformation of the original nonlinear power function. The allometric function for males ($W = 0.000731 \cdot \text{CL}^{3.024}$) was significantly different from that for females ($W = 0.000865 \cdot \text{CL}^{2.951}$), which strongly indicates the existence of dimorphic growth for pink shrimp.

Shrimp species of the family Penaeidae consistently rank among the top five economically important seafood products in the United States in terms of catch weight and dollar value (Iversen et al. 1993). During 1998, a total of 104,300 metric tons of penaeid shrimps, including white shrimp *Litopenaeus* (= *Penaeus*) *setiferus*, brown shrimp *Farfantepenaeus* (= *Penaeus*) *aztecus*, and pink shrimp *F.* (= *Penaeus*) *duorarum*, were landed in the southeastern United States, with an exvessel value of US\$423 million (NOAA 1999). Pink shrimp also play an important trophic role, serving as prey for numerous inshore coastal and coral reef fishes and birds (Bielsa et al. 1983).

The distribution of pink shrimp along U.S. coasts extends from North Carolina to the Dry Tortugas in Florida and thence along the Gulf of Mexico coast to Mexico's Yucatan Peninsula. Ow-

ing to the considerable fishing pressure on and high exploitation rates of pink shrimp stocks, accurate assessments are of critical importance to the management and sustainability of this resource. Thus, quantifying the relationships between animal size, density, and biomass are of central importance to both fisheries and ecological studies, particularly those analyzing community structure and function from bioenergetic or trophodynamic perspectives (Busacker et al. 1990; Ault et al. 1999b).

At present, shrimp stock assessments are conducted with either length-based or biomass-based methodologies because individuals are difficult or impossible to age, thereby precluding traditional age-based assessment methods (Garcia and Le Restre 1981; Pauly and Morgan 1987; Nance 1989; Sparre and Venema 1992; Anderson and Neumann 1996). Length-based assessment methodologies require accurate measurement of individuals' length and weight, along with the development of appropriate mathematical relationships between these variables to produce precise measures of population abundance. A number of studies of pink shrimp allometry (i.e., the relative growth of different body parts) have been conducted in various locations (Kutkuhn 1966; McCoy 1968, 1972; Fontaine and Neal 1971; Guitart and Reyes 1978; Hutchins et al. 1979; Campos and Berkeley 1986) and for many other penaeids (Chin 1960; Thomas 1975; Lares and Khandker 1976; Penn 1980; Devi et al. 1983). However, disagreement exists concerning the length measurements (e.g., total length versus carapace length), mathematical models (e.g., linear versus nonlinear), and parameter estimation procedures that are appropriate for quantifying allometric relationships. Most allometric functions have been developed for the exploited phase of the stock as they are typically derived from fishery-dependent data; for many crustaceans, however, these relationships are known to change at the onset of maturity (Hartnoll 1978, 1982). As a result, the allometry across the entire life cycle of shrimp remains poorly understood.

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The goal of this study was to use fishery-independent data from an efficient sampling program (Ault et al. 1999a) to provide accurate and precise allometric relationships among carapace length, total length, and wet weight for pink shrimp in Biscayne Bay, Florida. To accomplish this goal, we examined the effects of sex and maturity stage on allometry while identifying (1) appropriate mathematical functions for describing these relationships and (2) appropriate statistical procedures for fitting models to empirical data.

Methods

Biscayne Bay is a shallow (<5 m) subtropical bay of approximately 750 km² that is located in southeastern Florida adjacent to the city of Miami. Together with a network of coastal bays (e.g., Florida and Whitewater bays), Biscayne Bay serves as nursery grounds for the mature pink shrimp population residing in the Dry Tortugas region of the lower Florida Keys. Individual shrimp ranging from 3 to 30 mm in carapace length (CL) were obtained from Biscayne Bay during the course of a fishery-independent survey of the pink shrimp population (Ault et al. 1999a). Sampling for this study was conducted in November 1997 with a commercial live-bait shrimp vessel using a pair of roller frame trawls 3 m wide × 0.5 m high and outfitted with 10-mm-mesh nets. Additionally, a 3-mm-mesh hood was fitted over one of the nets to capture very small shrimp.

After capture, samples were frozen and then processed within a week. After thawing, a subsample was randomly obtained and individual shrimp were sexed and measured. An effort was made to have a representative sample size (n) for each 1-mm-CL category. Only individual shrimp with a complete rostrum were included. Sex was determined by the presence of a thelycum for females and a petasma for males (Perez Farfante 1970). Total length (TL) and CL were measured to the nearest 1 mm using a digital caliper. Carapace length was measured from the postorbital margin to the posterior margin of the carapace. Total length was measured in two different ways. First, following common practice, individuals were manually straightened by the observer to remove the natural curvature of the shrimp body, and TL was measured from the tip of the rostrum to the tip of the telson. Second, TL was measured along the shrimp's natural curvature by summing the lengths of five body portions: (1) the rostrum and carapace, (2) the first and second abdominal segments, (3) the third abdominal segment, (4) the

fourth, fifth, and sixth abdominal segments, and (5) the telson. At the study's outset, we conducted a pilot experiment to evaluate the reliability of measurements of CL, TL using the "straightened" method, and TL using the "curvature" method. Measurements of CL and TL were carried out on the same subset of individual shrimps by two different observers. Carapace length measurements were very consistent between the two observers, whereas straightened TL measurements were moderately consistent and curvature TL measurements were very inconsistent. We subsequently used the straightened method for measuring TL, and we chose CL as the explanatory (i.e., independent) variable for developing allometric relationships because it was the easiest, fastest, and most reliable length measurement to obtain. Wet weight (W) was determined to the nearest 0.01 g using a digital balance. Maturity stage was based on animal size following Eldred et al. (1961). Individuals with CL less than 18 mm were considered juveniles, while those with CL of 18 mm or more were considered subadults who had initiated maturation of the gonads.

The usual model for describing the average relationship between TL and CL for crustaceans is the linear function $TL = b_0 + b_1CL$ (e.g., McCoy 1972; Penn 1980). On the other hand, the average W -CL allometric relationship is usually described by the nonlinear power function $W = \alpha CL^\beta$. These functions were selected as the initial models for the TL-CL and W -CL relationships, respectively. In each case, final model selection and parameter estimation were guided by the general procedure described by Neter et al. (1996): (1) the mean trends of the data were examined for conformity to the proposed model form (i.e., linear or nonlinear); (2) the variance structure was examined for normality and homogeneity; and (3) a parameter estimation procedure (e.g., ordinary least-squares [OLS] regression or nonlinear regression) was chosen to match the combination of (1) and (2). Statistical analyses were conducted using SAS (SAS Institute 1990).

Differences in the TL-CL and W -CL relationships were examined between males and females and between juveniles and subadults by means of analysis of covariance (ANCOVA; Sokal and Rohlf 1981). An α -level of 95% was chosen for all statistical procedures.

Results

Altogether, 927 pink shrimp were measured, weighed, and sexed, resulting in a sample com-

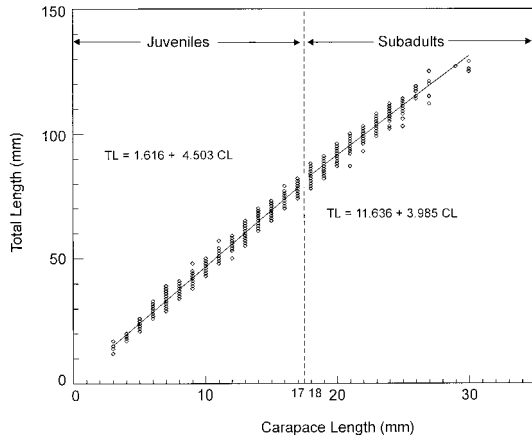


FIGURE 1.—Plots of the observations of total length (TL) and carapace length (CL) and the fitted relationships for juvenile (CL < 18 mm) and subadult (CL ≥ 18 mm) pink shrimp.

posed of 320 juvenile males (3–17 mm CL), 326 juvenile females (3–17 mm CL), 120 subadult males (18–27 mm CL), and 161 subadult females (18–30 mm CL).

TL–CL Relationship

We examined the TL–CL relationship using the linear statistical model

$$TL_i = b_0 + b_1CL_i + \epsilon_i, \quad (1)$$

where b_0 is the intercept parameter, b_1 is the slope parameter, and ϵ_i is the residual error of the i th observation. For each sex within each life stage, the average TL–CL relationship was linear, and error residuals followed a normal probability distribution (Shapiro–Wilk test, $P > 0.9$; Shapiro and Wilk 1965) and exhibited homogeneous variance along the range of CL. We selected the above equation as an appropriate TL–CL model and used

TABLE 1.—Regression coefficients for the estimation of total length (for juveniles and subadults) and weight (for males and females) from carapace length. The equations for total length are linear (equation 1 in the text), those for weight log-linear (equation 4). Values in parentheses are the standard errors of the coefficients.

Category	<i>n</i>	Intercept	Slope	<i>r</i> ²
Total-length model				
Juveniles	646	1.616 (0.247)	4.503 (0.021)	0.986
Subadults	281	11.636 (1.182)	3.985 (0.055)	0.949
Weight model				
Males	440	−7.221 (0.038)	3.024 (0.015)	0.990
Females	487	−7.052 (0.033)	2.952 (0.013)	0.989

OLS regression (Neter et al. 1996) to estimate model parameters.

Analysis of covariance detected no significant differences in the TL–CL relationship between juvenile males and females (for the slope coefficients, $F_{1, 642} = 1.10, P = 0.2939$) or between subadult males and females ($F_{1, 277} = 0.45, P = 0.5036$). Models were subsequently fitted to pooled male and female observations for each life stage (Figure 1; Tables 1, 2). The two estimated equations were $TL = 1.616 + 4.503 \cdot CL$ for juveniles and $TL = 11.636 + 3.985 \cdot CL$ for subadults. The TL–CL relationship changed at the onset of maturity. We found a significant decrease in the slope ($F_{1, 923} = 96.46, P = 0.0001$) and a corresponding increase in the intercept ($F_{1, 925} = 40,613.23, P = 0.0001$) for subadults compared with juveniles. In addition, comparisons of residual sums of squares (Somerton 1980) indicated that two separate linear TL–CL models, one for each life stage (Figure 1; Table 1), fit the data better than a single linear model applied over the entire CL range. The same test also indicated that separating juveniles from subadults at 18 mm CL pro-

TABLE 2.—Relationships between total length (TL) and carapace length (CL) for pink shrimp reported by various studies. The coefficients b_0 and b_1 are the intercept and slope of the linear model $TL = b_0 + b_1CL$ in all studies except Kutkuhn (1966), where they are the coefficients of the power function $TL = b_0CL^{b_1}$.

Study	Location	Date	Carapace length (mm)	<i>n</i>	Coefficients	
					b_0	b_1
This study	Biscayne Bay, Florida	Nov 1997	3–17	646	1.616	4.503
			18–30	281	11.636	3.985
Campos and Berkeley (1986)	Biscayne Bay, Florida	Dec 1984–Jul 1985	8–31	255	12.93	4.01
McCoy (1972)	Core and Bogue sounds, North Carolina	Sep 1969–Jul 1972	15–40	♂ = 297 ♀ = 503	12.37 21.90	3.81 3.40
Kutkuhn (1966)	Biscayne Bay and Dry Tortugas, Florida	Aug 1960–Jan 1961	♂ = 7–48	♂ = 729	5.27	0.96
			♀ = 7–52	♀ = 688	6.14	0.90

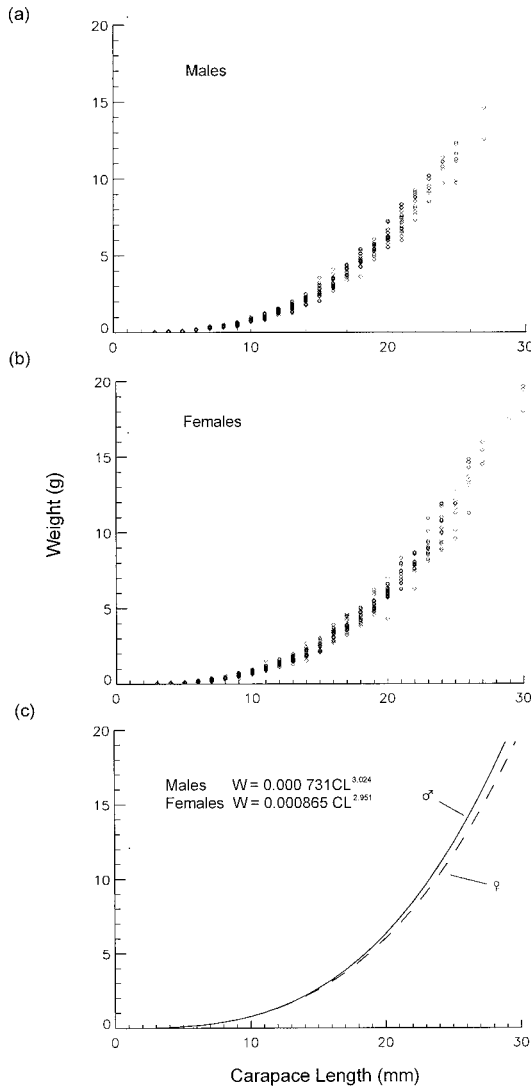


FIGURE 2.—Plots of the observations of weight (W) and carapace length (CL) for (a) male and (b) female pink shrimp, with (c) the fitted power relationships between weight and carapace length for the two sexes.

vides a better fit than separating them at any other carapace length.

W-CL Relationship

The average trend of the $W-CL$ observations conformed to a nonlinear power function for both male (Figure 2a) and female (Figure 2b) pink shrimp; however, the variance of the weight observations appeared to increase with increasing CL . Two statistical models with differing error assumptions were evaluated. The first is the additive error model,

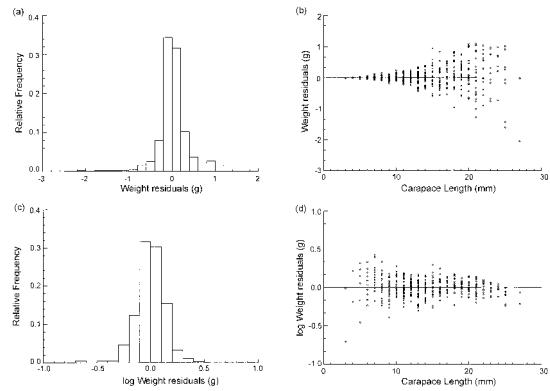


FIGURE 3.—Error residual analyses for the additive-error (equation 2 below; panels a and b) and multiplicative-error (equation 4; panels c and d) models of the relationship between weight and carapace length for male pink shrimp. Panels (a) and (c) present frequency histograms for the error residuals of the two models, panels (b) and (d) plots of the residuals against carapace length.

$$W_i = \alpha CL_i^\beta + \epsilon_i, \tag{2}$$

where α and β are parameters and ϵ_i is the residual error term. Model parameters were estimated by nonlinear regression (Seber and Wild 1989), which, like standard OLS regression, assumes that residual errors are normally distributed with homogeneous variance. The second model that we evaluated is the multiplicative error model,

$$W_i = \alpha CL_i^\beta E_i, \tag{3}$$

where E_i is the residual error term. For estimation purposes, it is convenient to transform both sides of equation (3) using the natural logarithm function to obtain the linear model

$$\log_e W_i = a + \beta \cdot \log_e CL_i + \epsilon_i, \tag{4}$$

where $a = \log_e \alpha$ and $\epsilon_i = \log_e E_i$. The parameters of equation (4) were estimated by OLS regression with the usual assumptions of normality and constant variance of residual errors. The power function parameter α (equation 3) was obtained via back-transformation. Analyses of error residuals for the two $W-CL$ models (equations 2 and 4) fitted to male pink shrimp observations are presented in Figure 3. While both models satisfied the normality assumption (Figures 3a, c; Shapiro-Wilk test, $P > 0.8$), the variance of the residuals was clearly heterogeneous along the range of CL (Figure 3b) for the additive-error $W-CL$ model (equation 2). Log-transformation appeared to correct this problem, yielding a fairly homogeneous

TABLE 3.—Relationships between weight (W) and carapace length (CL) for different species of penaeid shrimps reported by various studies. The coefficients α and β are the parameters of the power function $W = \alpha CL^\beta$.

Study	Species	Location	Date	Carapace length (mm)	n	Coefficients	
						α	β
This study	Pink shrimp	Florida	Nov 1997	$\delta = 3-27$	$\delta = 440$	0.000731	3.024
				$\text{♀} = 3-30$	$\text{♀} = 487$	0.000865	2.951
McCoy (1972)	Pink shrimp	North Carolina	Oct 1969–Jul 1972	15–40	$\delta = 297$	0.00148	2.77
					$\text{♀} = 503$	0.00209	2.66
McCoy (1972)	Brown shrimp	North Carolina	Oct 1969–Jul 1972	$\delta = 12-40$	$\delta = 259$	0.000819	2.94
				$\text{♀} = 12-40$	$\text{♀} = 243$	0.00113	2.84
Penn (1980)	Redspot king shrimp <i>Melicertus longistylus</i>	Australia	1971–1977	$\delta = 20-33$	$\delta = 45$	0.00110	2.81
				$\text{♀} = 19-35$	$\text{♀} = 45$	0.00140	2.72
Thomas (1975)	Green tiger shrimp <i>Penaeus semisulcatus</i>	India	Apr 1967–Mar 1969	$\delta = 15-46$	$\delta = 645$	0.9093	2.95
				$\text{♀} = 22-50$	$\text{♀} = 626$	1.5492	2.42

residual variance (Figure 3d) for the multiplicative-error model (equation 4). The results of residual analyses were identical for females. We thus selected the multiplicative-error model (equations 3 and 4) as the appropriate one for pink shrimp.

Analysis of covariance detected significant differences between the W –CL relationships for juvenile males and females (for β , $F_{1,436} = 8.69$, $P = 0.0033$; for α , $F_{1,438} = 34,965.71$, $P = 0.0001$). For subadults, significant differences were detected between the intercepts of the models for males and females ($F_{1,279} = 4,570.49$, $P = 0.0001$) but not the slopes ($F_{1,277} = 3.50$, $P = 0.0626$). Based on these results, separate W –CL models were estimated for each sex over the entire CL range (Figure 2c; Tables 1, 3). The allometric function for males was $W = 0.000731 \cdot CL^{3.024}$, that for females $W = 0.000865 \cdot CL^{2.951}$. These combined life stage W –CL relationships were significantly different (for the slope, $F_{1,923} = 29.3$, $P = 0.0009$; for the intercept, $F_{1,925} = 95,193.51$, $P = 0.0001$), indicating the presence of dimorphic growth. In addition, the rate parameter β (equation 3) was not significantly different from 3 for males (t -test, $P > 0.05$), indicating an isometric W –CL relationship; however, for females this relationship appears to be allometric (t -test, $P < 0.001$).

Discussion

A change in allometry between juvenile and subadult pink shrimp was indicated by an 11.5% decrease in the slope (parameter b_1) of the TL–CL relationship (Figure 1; Table 1). Because TL is essentially the sum of CL and the abdomen (i.e., tail) length, a decrease in the slope of the TL–CL relationship indicates that the carapace grows fast-

er relative to the abdomen in subadults than in juveniles. In penaeids, CL is defined as the length of the cephalothorax, which houses most of the internal organs, including major portions of the ovaries and testes of fully mature females and males (Solis 1988). The abdomen, in contrast, only contains a minor portion of the gonads. The shift in the TL–CL relationship that we found in pink shrimp thus appears to reflect the changing biological requirements of individuals reaching sexual maturity. Moreover, this shift in allometry is accompanied by a shift in habitat preference in which pink shrimp subadults move out of near-shore sea grass beds (the primary juvenile habitat) in preparation for emigration from Biscayne Bay to offshore spawning grounds (Ault et al. 1999a). Abrupt shifts in allometry associated with sexual maturation have been reported for many types of crustaceans, including cladocerans, isopods, amphipods, and at least two decapod subgroups, brachyuran crabs and clawed lobsters (Hartnoll 1982). Our results indicate that this phenomenon extends to penaeid shrimps, another decapod subgroup.

We modeled the TL–CL relationship for pink shrimp as two separate linear functions (equation 1), one for juveniles and another for subadults. This approach differs from that of previous pink shrimp investigations (Table 2). McCoy (1972) and Campos and Berkeley (1986) developed single linear functions that are in general agreement with our relationship for subadults. Their studies did not target smaller juveniles. Our analysis shows that a single linear function cannot account for the shift in the TL–CL relationship that occurs at the onset of sexual maturity and thus will yield in-

accurate conversions between TL and CL if applied to both juveniles and subadults (Figure 1). Kutkuhn (1966) employed a nonlinear hyperbolic function to capture the change in the TL–CL relationship as pink shrimp individuals increase in length (Table 2). This implies that the shift in allometry between juveniles and subadults occurs in a continuous, gradual manner. Our model, in contrast, presumes that the allometric change occurs at a pubertal molt and is better described as a discrete switch between separate linear phases (Figure 1). This “two-phase” model appears to be well suited for describing a variety of allometric length relationships (e.g., chelar length–carapace length, abdomen width–carapace width, and so forth) across a wide spectrum of crustaceans (Hartnoll 1982). It has also been employed in connection with other aspects of crustacean growth, most notably in models of molt increment (Somerton 1980). We found no sex differences in the TL–CL relationship by life stage. Both McCoy (1972) and Kutkuhn (1966) developed separate TL–CL models for female and male pink shrimp (Table 2). These investigations sampled larger (presumably fully mature) adults than did the present study. It is therefore possible that sex differences in the TL–CL relationship become apparent in the reproductively mature adult phase; however, neither author reported statistical analyses to warrant development of sex-specific functions.

In contrast to our findings for the TL–CL relationship, we detected significant differences in the W –CL relationship between male and female pink shrimp. The rate parameter β (equation 3) for males was higher than that for females; consequently, male pink shrimp become progressively heavier than females at a given carapace length as they grow (Figure 2c). This phenomenon has been observed in pink shrimp in North Carolina (McCoy 1972) as well as in other penaeids (Table 3). Our life-stage-specific analysis provides additional insight into this differential growth process. For juveniles, both the intercept (a) and slope (β) parameters of the log-transformed W –CL model (equation 4) differed by sex, but only the intercept differed between female and male subadults. These results suggest that although sex-specific differences in the W –CL relationship occur during the juvenile growth phase ($CL < 18$ mm), these differences only become apparent (Figure 2c) after the onset of sexual maturation ($CL \geq 18$ mm).

Our ability to detect sex-specific differences in the pink shrimp W –CL relationship was enhanced by judicious choices of both the estimation model

(equation 4) and the explanatory variable (CL). The steadily increasing variance in weight with increasing carapace length (e.g., Figures 2a, 3b) dictated our selection of the multiplicative-error model (equation 3) over the additive-error model (equation 2) for both male and female pink shrimp. Subsequent application of the \log_e – \log_e transformation methodology (Carroll and Ruppert 1988) simultaneously linearized the function (equation 4) and stabilized the residual variance (Figure 3d). These model attributes allowed for the use of OLS regression for parameter estimation and ANCOVA for statistical testing. Log-transformed models have been the traditional choice in fishery science for estimating weight–length relationships (Ricker 1975), including those for penaeid shrimps (Chin 1960; Thomas 1975; Penn 1980). It should be noted, however, that emphasis has been placed on linearizing the model function (e.g., Ricker 1975; Sparre and Venema 1992), with little attention being paid to the variance properties (e.g., additive or multiplicative, normal or nonnormal). Thus, while our results support the use of equation (4) as a weight–length estimation model, it is unknown whether this has been an appropriate choice in other studies.

To keep the measurement error of the explanatory variable at a minimum, we chose CL over TL. Problems similar to ours in reliably measuring TL have been analyzed and discussed by many penaeid researchers (Chin 1960; Kutkuhn 1966; McCoy 1972; Thomas 1975) and have led to the use of CL as the standard length measure in growth studies of lobsters (Cobb and Wang 1985), a harvested decapod group with morphology similar to that of shrimps. Unfortunately, there appears to be no consensus among investigators for a standard unit of length in penaeid growth studies, as evidenced by the continued use of a variety of length variables, including TL (Fontaine and Neal 1971; Lares and Khandker 1976; Hutchins et al. 1979; Devi et al. 1983), CL (this study), and hybrids of these measures (Guitart and Reyes 1978).

Seasonal variation in allometry was controlled in our study by conducting field sampling during a single month, in contrast to many other investigations (Tables 2 and 3). Our attempts to minimize the variation at each research step—sampling, measuring, and modeling—appear to have been successful, as we were able to elucidate fairly subtle biological aspects of pink shrimp allometry that may otherwise have been masked by excessive measurement or model error. This study also provides a starting point for addressing additional fac-

ets of allometry relevant to pink shrimp resource management, namely, variation in allometry among seasons within an area and among populations in different geographical regions.

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