Modeling Growth-Time And Weight-Length Relationships In a Single Year-Class Fishery

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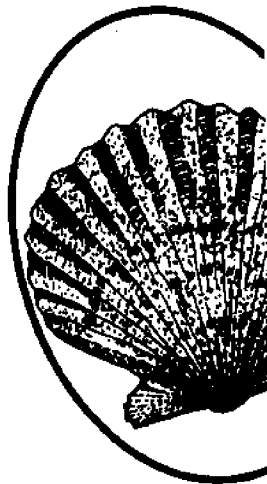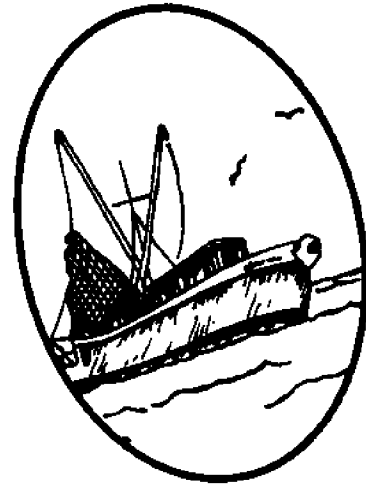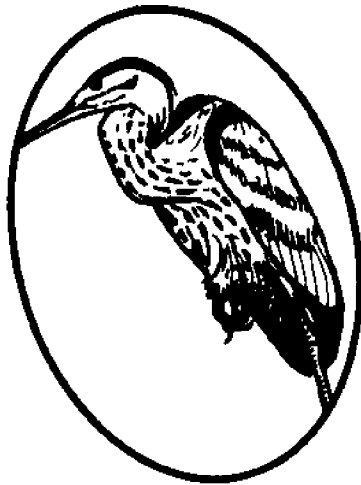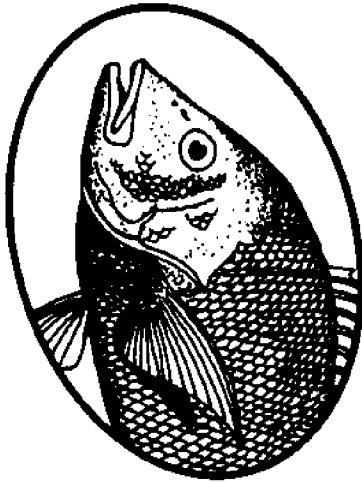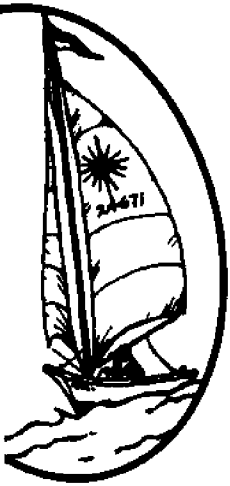
MODELING GROWTH-TIME and WEIGHT-LENGTH RELATIONSHIPS

IN A SINGLE YEAR-CLASS FISHERY WITH EXAMPLES FOR

NORTH CAROLINA PINK AND BROWN SHRIMP

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ABSTRACT

This paper presents an extension of the classical concepts of growth over time and of a weight-length relationship for a single year-class fishery that explicitly accounts for the stochastic variation known to exist in such a population. It also shows how the extended conceptualization enables one to look at alternative characterizations of a fish population that can be useful when deciding whether or not to allow fishing. Techniques for estimating the extended models efficiently are described, as are procedures for testing for differences in growth and weight-length parameters based on sex and subspecies. The potential use of these models to facilitate the quantification of population biomass is also presented. Data on North Carolina pink and brown shrimp are used to illustrate the concepts and models. Algorithms for effecting several of the proposed procedures are included.

1. Introduction[†]

Two relationships of special importance in the study of a fish species concern the way in which a fish grows over time and the way in which its weight relates to its length. The scholarly literature on these topics (Beverton and Holt, (1957) and Ricker, (1958)) encourages one to study growth via the von Bertalanffy growth curve

$$L_t = L_\infty(1 - e^{-Kt}) \tag{1.1}$$

where L_t denotes length at time t, L_∞ denotes the length of a fish at maturity and K denotes the growth rate. For the weight-length relationship, these sources suggest the expression

$$W = aL^b \quad , \tag{1.2}$$

W and L denoting weight and length respectively.

As conceptual devices, these expressions are helpful. Usually, they describe central tendency or mean value behavior. However, they leave considerable room for improvement when one needs to represent growth and biomass in a model designed to approximate real world behavior. In particular, (1.1) and (1.2) do not acknowledge stochastic variation which one expects to observe when studying individual fish. Also, they provide no explicit construction for moving from observable characteristics of individual fish to an aggregate representation of biomass.

[†]See Section 9 for an exhaustive list of definitions.

The purposes of this paper are:

1. To extend the conceptual representations in (1.1) and (1.2) to account for stochastic variation in a single year-class fishery.

2. To show how the extended conceptualization enables one to look at alternative characterizations of a fish population.

3. To describe the estimation of the parameters of the extended models in a statistically efficient manner.

4. To describe how one tests for differences in growth and weight-length parameters based on sex and subspecies.

5. To sketch how the extended models with their estimated parameters facilitate the characterization of biomass of a species.

6. To illustrate the proposed extensions and techniques, using data from tagging studies by McCoy and Brown (1967), McCoy (1968) and McCoy (1972) on North Carolina pink and brown shrimp.

The impetus for this work arose in the course of building a model to study how several alternative shrimp management policies would affect the performance of the North Carolina shrimp fishery. Preliminary analysis indicated that using (1.1) and (1.2) without accounting for stochastic variation would fail to capture the variation in growth, weight and length known to exist among shrimp of a given species within a year. In the course of modeling, it also became necessary to develop migration and catch-effort relationships that acknowledge stochastic variation explicitly. These migration and catch-effort models will be described methodologically and illustrated with an example in a subsequent technical report.

2. Growth in a Stochastic Setting

Let

t_0 = tagging and release date

L = length of fish at release date

t_1 = recapture date

L_t = length of fish on date $t > t_0$.

Consider the model

$$L_t = \alpha + \beta L_{t-1} + U_t \qquad\qquad t = t_0 + 1,\ t_0 + 2,\ \ldots \qquad (2.1)$$

where $\alpha > 0$, $0 < \beta < 1$ and $\{U_t;\ t = t_0 + 1,\ t_0 + 2,\ \ldots\}$ is a sequence of independent identically distributed (i.i.d.) random innovations each having the normal distribution with mean 0 and variance[†] $\sigma^2 > 0$. This last characterization implies

$$\text{pr}(U_t \leq x) = \Phi(x/\sigma) = \int_{-\infty}^{x/\sigma} \phi(y)\,dy$$

$$\phi(y) = \frac{1}{\sqrt{2\pi}}\, e^{-y^2/2} \qquad . \tag{2.2}$$

If one could track a fish from t_0 to t_1 , one could obtain the lengths $L_{t_0+1},\ \ldots,\ L_{t_1}$ to estimate α, β and σ^2 . However, the availability of only the more limited data L, t_0, L_{t_1} and t_1 suggests an alternative approach. In particular, one can write (2.1) in the form

$$L_t = \lambda + (L-\lambda)\beta^{t-t_0} + V_t \tag{2.3a}$$

[†]An innovation at time t can be viewed in this case as a deviation from the mean length at time t .

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where

$$V_t = \sum_{s=0}^{t-t_0-1} \beta^s U_{t-s} \qquad\qquad t = t_0+1, t_0+2, \ldots \qquad\qquad (2.3b)$$

$$\lambda = \frac{\alpha}{1-\beta} \qquad .$$

Here λ denotes the mean length of a mature fish, often referred to as L_∞ (Beverton and Holt, 1957, p. 32). Also, V_t has the normal distribution with mean zero and variance

$$\text{var}(V_t) = \frac{\sigma^2[1-\beta^{2(t-t_0)}]}{1-\beta^2} \qquad . \qquad\qquad (2.4)$$

In practice, (2.3a) is considerably more enlightening that (2.1) is. For example, for a fish of initial length L, the mean length of L_t is

$$\mu_t(L,t_0) = \lambda + (L-\lambda)\beta^{t-t_0} \qquad\qquad (2.5)$$

and its variance is

$$\sigma_t^2(L,t_0) = \text{var}(V_t) \qquad . \qquad\qquad (2.6)$$

For a mature fish this implies

$$\lim_{t\to\infty} \text{pr}(L_t \le x | L, t_0) = G_0(x) = \Phi\left(\frac{x-\lambda}{\sigma/\sqrt{1-\beta^2}}\right) \qquad\qquad (2.7)$$

and more generally

$$\text{pr}(L_t \le x | L, t_0) = G_4(x) = \Phi\left(\frac{x-\mu_t(L,t_0)}{\sigma_t(L,t_0)}\right) \qquad . \qquad\qquad (2.8)$$

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Suppose that in a tagging-recapture experiment L differs among fish. In particular, assume that L has the normal distribution with mean $\mu(L)$ and variance $\sigma^2(L)$. Then the length of a randomly selected fish at time t is normally distributed with mean and variance

$$\mu_t(t_0) = \lambda + [\mu(L) - \lambda]\beta^{t-t_0}$$

$$(2.9)$$

$$\sigma_t^2(t_0) = \sigma^2(L)\beta^{2(t-t_0)} + var(V_t) \quad ,$$

respectively, so that

$$pr(L_t \leq x|t_0) = G_8(x) = \Phi\left(\frac{x-\mu_t(t_0)}{\sigma_t(t_0)}\right) \quad . \qquad (2.10)$$

Expressions (2.7), (2.8) and (2.10) provide the basis for many alternative descriptive factors regarding length, some of which appear in Table 1.

Mixing Males and Females

The results in Table 1 apply for a single species and sex. If in a given species male and female fish exhibit identical α, λ and σ^2 then Table 1 continues to apply. Generally at least one, if not all three, parameters differ for males and females, and the formulae in Table 1 need modification. Let

$$G_{i,j}(x) \qquad i = 0,4 \text{ and } 8 \quad j = 1,2 \qquad (2.11)$$

denote the distribution functions for females $(j = 1)$ and males $(j = 2)$. Then a randomly sampled fish has distribution

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Table 1

Probabilistic Characterizations of a Fish Population

Probability at time t	i	Mature[a]	i	Tagged Conditional[b]	i	Tagged Unconditional[c]
pr(length $\leq x$)	0	$G_0(x)$	4	$G_4(x)$	8	$G_8(x)$
pr(maximal length of N fish $\leq x$)	1	$[G_0(x)]^N$	5	$[G_4(x)]^N$	9	$[G_8(x)]^N$
pr(minimal length of N fish $\geq x$)	2	$1 - [1-G_0(x)]^N$	6	$1 - [1-G_4(x)]^N$	10	$1 - [1-G_8(x)]^N$
pr(M fish have length $\leq x$ and N-M fish have length $\geq x$) $M = 0,1,\ldots,N$	3	$\binom{N}{M}[G_0(x)]^M[1-G_0(x)]^{N-M}$	7	$\binom{N}{M}[G_4(x)]^M[1-G_4(x)]^{N-M}$	11	$\binom{N}{M}[G_8(x)]^M[1-G_8(x)]^{N-M}$

[a]Denotes fully grown fish.

[b]Denotes fish in a tagging experiment all with initial length L at t_0.

[c]Denotes fish in a tagging experiment in which the initial length of each fish is a normal random variable with mean $\mu(t_0)$ and variance $\sigma^2(t_0)$.

$$\tilde{G}_i(x) = \rho G_{i,1}(x) + (1-\rho)G_{i,2}(x) \qquad\qquad 0 \le \rho \le 1 \qquad (2.12)$$

where ρ denotes the proportion of females in the population. Although $\rho = .05$ is a plausible assumption, biological considerations and empirical data may suggest an alternative value. To obtain the mixed distributions in Table 1, one substitutes $\tilde{G}_i(x)$ for $G_i(x)$ for $i = 0$, 4 and 8 . Table 2 presents several of these characterizations using estimates of β, λ and σ^2 for North Carolina pink female and male shrimp. Columns 1 and 2 show the cumulative distributions of length for a randomly selected mature female shrimp and mature male shrimp respectively. Column 3 shows the length distribution for a randomly selected mature pink shrimp regardless of sex.

Column 4 of Table 2 presents a distribution that can relate to the decision to fish. Suppose that this decision is based on collecting a sample of N fish regardless of sex. If at least M fish in the sample are at least x millimeters in length, the decision is to fish. Otherwise, the decision is not to fish. Since the decision is based on a sample, it is conceivable that these data may fail to support the decision to fish when, in fact, a complete census (which is not possible) of the fish population would justify fishing. Assume N = 100 and M = N/2 = 50 . To assess the potential for a correct decision, Column 4 of Table 2 lists the probability that at least 50 percent of the mature shrimp in a random sample of 100 are at least x millimeters in length. Note that if x = 170 millimeters were the economically determined criterion for allowing fishing in general, then a correct decision would occur only 15.8 percent of the time. Since the populations generally encountered are not entirely mature, the probability of a correct decision would be even less than this in practice. If the economically

Table 2

Table 2
Characterizations for Mature North Carolina
Pink Shrimp[a]

Length x (millimeters)	Probability that a randomly selected shrimp is $\leq x$ in length			Probability that at least M of N randomly selected mature shrimp (regardless of sex) have length of at least x ($N = 100$, $M = 50$)
	Female $G_{0,1}(x)$	Male $G_{0,2}(x)$	Mixed $\tilde{G}_0(x)$	$\sum_{i=M+1}^{N} \binom{N}{i} [\tilde{G}_0(x)]^i [1-\tilde{G}_0(x)]^{N-i}$
	(1)	(2)	(3)	(4)
110	.000	.000	.000	1.000
115	.000	.005	.002	1.000
120	.000	.032	.016	1.000
125	.000	.130	.065	1.000
130	.000	.342	.171	1.000
135	.000	.623	.311	.999
140	.000	.848	.424	.948
145	.000	.960	.480	.691
150	.001	.993	.497	.562
155	.005	.999	.502	.523
160	.017	.999	.508	.473
165	.047	.999	.523	.356
170	.109	.999	.555	.158
175	.218	1.000	.609	.017
180	.370	1.000	.685	.000
185	.547	1.000	.773	.000
190	.714	1.000	.857	.000
195	.845	1.000	.922	.000
200	.928	1.000	.964	.000
205	.972	1.000	.986	.000
210	.991	1.000	.995	.000
215	.997	1.000	.998	.000
220	.999	1.000	.999	.000
225	.999	1.000	.999	.000

[a]For the distribution $G_{i,j}(x)$, the i subscript denotes the relevant distribution from Table 1 and the j subscript denotes sex. In particular, $j = 1$ denotes females and $j = 2$, males. The notation $\tilde{G}_i(x)$ refers to distribution i from Table 1 for equal percentages of male and female shrimp in a population.

determined criterion is $x = 140$ millimeters, then a correct decision occurs with virtual certainty. This example is one illustration of the characterizations available through Table 1.

Computing a $G_i(x)$

Formulae for evaluating $\phi(\cdot)$, and thereby $G_i(\cdot)$ for $i = 0, 4$ and 8 appear in Abramovitz and Stegun (1964). However, a more direct method, when coding in the FORTRAN programming language, uses FORTRAN's built-in error function ERF($\cdot$) . Algebraically the error function is

$$e(z) = \frac{2}{\sqrt{\pi}} \int_0^z e^{-y^2} \, dy \qquad\qquad 0 \leq z < \infty \qquad\qquad (2.13)$$

so that

$$\phi(z) = \begin{cases} 0.5 - \dfrac{e(|z|/\sqrt{2})}{2} & -\infty < z \leq 0 \\[3em] 0.5 + \dfrac{e(z/\sqrt{2})}{2} & 0 \leq z < \infty \end{cases} \qquad\qquad (2.14)$$

In a FORTRAN program one need only substitute ERF($\cdot$) for e($\cdot$) . Once $G_i(x)$ for $i = 0, 4$ and 8 are computed, the computations of $G_i(x)$ for $i \neq 0, 4$ and 8 use the formulae in Table 1.

Quantiles

Probability distributions can provide considerable useful information for characterizing a fish population. This is especially true when one takes the extra steps to look at the quantiles of the distribution. Let G_i denote

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a cumulative distribution on length. Then its pth quantile is

$$Q_i(p) = \min[x: \quad p \leq G_i(x)] \qquad 0 < p < 1 \quad . \qquad (2.15)$$

For example $p = 0.5$ yields the median $Q_i(0.5)$. Note that for $p = 0.5$

$$Q_0(0.5) = \mu(t_0) \qquad . \qquad (2.16)$$

However,

$$Q_1(0.5) \neq \mu(t_0) \qquad . \qquad (2.17)$$

This is an important point, since one often focuses on the large members of a fish sample whose distributional characteristics *differ* from those of a randomly selected fish. Table 3 lists selected quantiles for male and female pink shrimp taken in North Carolina waters, using $N = 100$ and assuming $p = 0.5$. For management purposes, an analysis based on quantiles may occasionally be more appropriate than one restricted to the data in Columns 1, 2 and 3 of Table 2. This is so because managers have an understanding of the commercial meaning of length. For example, note than the median length of a randomly selected mature shrimp is 152.34 mm. That is, 50 percent of a random sample of mature shrimp would exceed 152.34 mm. in length. However, if one were to examine the largest shrimp in many successive batches of $N = 100$, the median length would be 208.22 mm. This means that in 50 percent of the samples, the largest shrimp would exceed 208.22 mm. in length. The issue of importance here is whether one wants to characterize a population by a randomly selected member or by the largest member in a randomly selected sample.

The binary search in algorithm Q provides a relatively simple method of computing $Q_i(p)$:

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Table 3

Selected Quantiles for Mature North Carolina Pink Shrimp[a]

N = 100 and ρ = 0.5

p	Length of a Randomly Selected Shrimp			Maximal Length in a Sample of 100 Shrimp		
	Female $Q_{0,1}(p)$	Male $Q_{0,2}(p)$	Mixed $\tilde{Q}_0(p)$	Female $Q_{1,1}(p)$	Male $Q_{1,2}(p)$	Mixed $\tilde{Q}_1(p)$
.05	165.28	121.33	123.90	204.71	145.93	201.11
.10	169.43	123.90	126.95	205.96	146.72	202.51
.20	174.31	126.98	131.10	207.58	147.73	204.31
.30	177.85	129.18	134.58	208.83	148.52	205.71
.40	180.84	131.07	138.67	209.99	149.24	206.97
.50	183.65	132.84	152.34	211.12	149.94	208.22
.60	186.52	134.58	174.31	212.31	150.69	209.53
.70	189.51	136.47	180.90	213.65	151.53	210.99
.80	193.30	138.67	186.52	215.36	152.58	212.82
.90	197.99	141.72	193.11	217.95	154.20	215.57
.95	201.90	144.42	197.99	220.21	155.64	218.01

[a] $Q_{i,j}(p) = \min[x:\ p \leq G_{i,j}(x)]$ for $i = 0,1$ and $j = 1,2$.

$\tilde{Q}_i(p) = \min[x:\ p \leq \tilde{G}_i(x)]$ for $i = 0,1$. See Table 2 for definitions of $G_{i,j}(x)$ and $\tilde{G}_i(x)$.

Algorithm Q (p, L^*, δ)

1. $\tilde{L} \leftarrow 0$.

2. $\tilde{U} \leftarrow L^*$.

3. $x \leftarrow (\tilde{L} + \tilde{U})/2$.

4. If $|p - G(x)| \leq \delta$, x is the desired quantile.

5. If $p < G(x)$, $\tilde{U} \leftarrow x$ and go to 3 .

6. $\tilde{L} \leftarrow x$.

7. Go to 3.

3. Maximum Likelihood Estimation for Growth Curves

This section describes one way of applying the maximum likelihood method to the estimation of the growth rate β, the mean length at maturity λ and the measure of variation σ^2. The method is known to make the most efficient use of the sample data, both in estimation and in hypothesis testing.

Let

$\qquad$ X = length on tag-release date

$\qquad$ Y = length on recapture date

$\qquad$ Z = elapsed time in weeks (or fraction thereof) between release and capture

$\qquad$ N = number of fish in a sample.

Define $\beta(x) = \beta^x$ and

$$g(\beta,\lambda,\sigma^2|X,Y,Z) = \sqrt{\frac{1-\beta(2)}{2\pi\sigma^2[1-\beta(2Z)]}} \; \exp\left\{-\frac{[Y-\lambda(1-\beta(Z))-X\beta(Z)]^2}{2\sigma^2[1-\beta(2Z)]/[1-\beta(2)]}\right\} \quad (3.1)$$

and let the subscripts i denote subspecies; j, sex; and k, the kth in a sample of N_{ij} fish of subspecies i and sex j. Also, let $\underline{\omega}_{ij} = (\beta_{ij}, \lambda_{ij}, \sigma^2_{ij})$, $\underline{\omega} = (\underline{\omega}_{11}, \underline{\omega}_{12}, \underline{\omega}_{21}, \underline{\omega}_{22})$ and

$$h_{ij}(\underline{\omega}_{ij}) = \prod_{k=1}^{N_{ij}} g(\underline{\omega}_{ij}|X_{ijk}, Y_{ijk}, Z_{ijk}) \; . \quad (3.2)$$

Then for two subspecies the *likelihood function* is

$$h(\underline{\omega}) = \prod_{i=1}^{2} \prod_{j=1}^{2} h_{ij}(\underline{\omega}_{ij}) \; . \quad (3.3)$$

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In practice, concentration on the *loglikelihood function*

$$m(\underline{\omega}) = \ln h(\underline{\omega}) = \sum_{i=1}^{2} \sum_{j=1}^{2} m_{ij}(\underline{\omega}_{ij}) \quad , \tag{3.4}$$

where

$$m_{ij}(\underline{\omega}_{ij}) = \ln h_{ij}(\underline{\omega}_{ij}) = \sum_{k=1}^{N_{ij}} \ln g(\underline{\omega}_{ij}|X_{ijk}, Y_{ijk}, Z_{ijk}) \quad , \tag{3.5}$$

facilitates analysis and computation. Therefore, without loss of generality, we concentrate on $m(\underline{\omega})$.

Let $\hat{\beta}_{ij}$, $\hat{\lambda}_{ij}$, and $\hat{\sigma}_{ij}^2$ be the values of β_{ij}, λ_{ij} and σ_{ij}^2, respectively, that maximize $m(\underline{\omega})$ and, therefore, $h(\underline{\omega})$. These estimators are known to have particularly attractive statistical properties. With regard to estimation they are consistent, which means that they converge to the true parameter values in probability as N_{ij} increases. For given large N_{ij}, they have minimum variance among all possible alternative estimators. With regard to hypothesis testing, they lead to a uniformly most powerful test of a null hypothesis H_0 against an alternative H_1. This means that the probability of rejecting H_0 when it is false is greater than the corresponding probability for any alternative test of this hypothesis. Moreover, the test is consistent, which means that this rejection probability when H_0 is false converges to unity as N_{ij} increases.

Let $\hat{\underline{\omega}}_{ij} = (\hat{\beta}_{ij}, \hat{\lambda}_{ij}, \hat{\sigma}_{ij}^2)$. Inspection of (3.4) reveals that when $m(\underline{\omega})$ is at its maximum

$$\left. \frac{\partial m_{ij}(\underline{\omega}_{ij})}{\partial \beta_{ij}} \right|_{\underline{\omega}_{ij} = \hat{\underline{\omega}}_{ij}} = 0 \qquad\qquad (3.6a)$$

$$\left. \frac{\partial m_{ij}(\underline{\omega}_{ij})}{\partial \lambda_{ij}} \right|_{\underline{\omega}_{ij} = \hat{\underline{\omega}}_{ij}} = 0 \qquad\qquad (3.6b)$$

$$\left. \frac{\partial m_{ij}(\underline{\omega}_{ij})}{\partial \sigma^2_{ij}} \right|_{\underline{\omega}_{ij} = \hat{\underline{\omega}}_{ij}} = 0 \qquad i,j = 1,2 \quad . \ (3.6c)$$

Define

$$A_{ijk}(\hat{\beta}) = \frac{Y_{ijk} - X_{ijk}\hat{\beta}(Z_{ijk})}{1 + \hat{\beta}(Z_{ijk})} \qquad\qquad (3.7a)$$

$$B_{ijk}(\hat{\beta}) = \frac{1 - \hat{\beta}(Z_{ijk})}{1 + \hat{\beta}(Z_{ijk})} \qquad\qquad (3.7b)$$

$$C_{ijk}(\hat{\beta},\hat{\lambda}) = \frac{\{Y_{ijk} - \hat{\lambda}[1-\beta(Z_{ijk})] - X_{ijk}\hat{\beta}(Z_{ijk})\}^2}{1 - \hat{\beta}(2Z_{ijk})} \qquad\qquad (3.7c)$$

where $\hat{\beta}(x) = \hat{\beta}^x$. Then explicit evaluation of (3.6a), (3.6b), and (3.6c) shows that

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$$\hat{\lambda}_{ij} = \frac{\sum\limits_{k=1}^{N_{ij}} A_{ijk}(\hat{\beta}_{ij})}{\sum\limits_{k=1}^{N_{ij}} B_{ijk}(\hat{\beta}_{ij})} \qquad (3.8a)$$

$$\hat{\sigma}_{ij}^2 = \frac{1 - \hat{\beta}_{ij}(2)}{N_{ij}} \sum\limits_{k=1}^{N_{ij}} C_{ijk}(\hat{\beta}_{ij}, \hat{\lambda}_{ij}) \qquad . \qquad (3.8b)$$

Note that $\hat{\lambda}_{ij}$ is a function of $\hat{\beta}_{ij}$ and that $\hat{\sigma}_{ij}^2$ is a function of $\hat{\lambda}_{ij}$ and $\hat{\beta}_{ij}$. To find $\hat{\underline{\omega}}_{ij}$ one can use an iterative procedure that exploits these relationships. Algorithm MLEG describes one such procedure that relies on a binary search to find $\hat{\beta}_{ij}$.

Algorithm MLEG

1. $\tilde{L} \leftarrow 0$.

2. $\tilde{U} \leftarrow 1$.

3. Initialize $\tilde{\beta}_{ij}$.

4. Compute $\tilde{\lambda}_{ij}$ using (3.8a).

5. Compute $\tilde{\sigma}_{ij}^2$ using (3.8b).

6. $\tilde{m}_{ij} \leftarrow m_{ij}(\tilde{\underline{\omega}}_{ij})$, which uses (3.5).

7. $\hat{\beta}_{ij} \leftarrow \dfrac{\tilde{L} + \tilde{U}}{2}$

8. Compute $\hat{\lambda}_{ij}$ using (3.8a).

9. Compute $\hat{\sigma}_{ij}^2$ using (3.8b).

10. Compute $m_{ij}(\hat{\underline{\omega}}_{ij})$ using (3.5).

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11. If $|\tilde{m}_{ij} - m_{ij}(\hat{\underline{\omega}}_{ij})| \leq \delta$ return with $\hat{\underline{\omega}}_{ij}$ and $m_{ij}(\hat{\underline{\omega}}_{ij})$.

12. If $\tilde{m}_{ij} > m_{ij}(\hat{\underline{\omega}}_{ij})$

    a. If $\tilde{\beta}_{ij} < \hat{\beta}_{ij}$, $\tilde{U} \leftarrow \hat{\beta}_{ij}$ and go to 7 .

    b. $\tilde{L} \leftarrow \hat{\beta}_{ij}$ and go to 7 .

13. $\tilde{m}_{ij} \leftarrow m_{ij}(\hat{\underline{\omega}}_{ij})$.

14. If $\tilde{\beta}_{ij} < \hat{\beta}_{ij}$, $\tilde{L} \leftarrow \tilde{\beta}_{ij}$ and go to 16 .

15. $\tilde{U} \leftarrow \tilde{\beta}_{ij}$.

16. $\tilde{\beta}_{ij} \leftarrow \hat{\beta}_{ij}$.

17. Go to 7 .

Although we currently have no proof that $h(\underline{\omega})$ is unimodal, experience with the shrimp data for several different initial values in $[0,1)$ in step 3 lead to the same final value for $\hat{\beta}_{ij}$. If one inclines to discard this experience, one should execute the coded algorithm for several different initial values in $[0,1)$ in step 3 and, if the final values of $\hat{\underline{\omega}}_{ij}$ differ, choose the vector with the largest value for $m(\hat{\underline{\omega}}_{ij})$. Table 4 lists maximum likelihood estimates for North Carolina pink and brown shrimp by sex.

Examining Length Residuals

Whenever one fits data to an assumed model such as (2.3) , some proof of the fit of the model is of seminal importance. Rewriting (2.3a) as

$$V_t = L_t - \lambda - (L_{t_0} - \lambda)\beta^{t-t_0} , \qquad (3.9)$$

one sees that V_t has mean zero and variance $\sigma^2[1 - \beta^{2(t-t_0)}]/(1-\beta^2)$. Then $V_t/\sqrt{\sigma^2[1-\beta^{2(t-t_0)}]/(1-\beta^2)}$ has mean zero and variance unity. If for

Table 4
Maximum Likelihood Growth Parameter Estimates for North Carolina Pink and Brown Shrimp by Sex[a]

	i	j	N_{ij}	$\hat{\beta}_{ij}$	$\hat{K}_{ij}$	$\hat{\lambda}_{ij}$	$\hat{\sigma}^2_{ij}$	$\hat{\alpha}_{ij}$	$m(\hat{\underline{\omega}}_{ij})$
Pink									
Female	1	1	37	.9048	.1000	183.68	22.51	17.48	-127.62
Male	1	2	216	.8903	.1162	132.83	10.02	14.57	-647.33
Brown									
Female	2	1	77	.8597	.1512	174.86	24.34	24.53	-257.89
Male	2	2	130	.6953	.3634	132.96	9.83	40.51	-359.41
Total Loglikehood Value									-1392.25

$^a\hat{\alpha}_{ij} = \hat{\lambda}_{ij}(1-\hat{\beta}_{ij})$; see (2.3c) . $\hat{K}_{ij} = -\ln\hat{\beta}_{ij}$; see (1.1) .

each fish one could observe the innovation V_t , normalize it by standard deviation and plot it versus $\lambda + (L_{t_0} - \lambda)\beta^{t-t_0}$, one should observe a plot of normally distributed random quantities with mean zero and variance unity. In particular, the plot would show no association between $\lambda + (L_{t_0} - \lambda)\beta^{t-t_0}$ and $V_t / \sqrt{\sigma^2[1-\beta^{2(t-t_0)}]/(1-\beta^2)}$. Any alternative picture would give reason for being suspicious of the data, the model or both.

Although one cannot observe V_t in practice, one can compute an approximation to it using the maximum likelihood results. Let us concentrate on

subspecies i and sex j . One prediction of the length of fish k in this sample is

$$\hat{Y}_{ijk} = \hat{\lambda}_{ij} + (X_{ijk} - \hat{\lambda}_{ij})\hat{\beta}_{ij}(Z_{ijk}) \quad . \tag{3.10}$$

We call

$$S_{ijk} = Y_{ijk} - \hat{Y}_{ijk} \tag{3.11}$$

the *residual* for fish k . Then one can show that the normalized residual

$$\tilde{S}_{ijk} = \frac{S_{ijk}}{\sqrt{\hat{\sigma}_{ij}^2 \left[\dfrac{1-\hat{\beta}_{ij}(2Z_{ijk})}{1-\hat{\beta}_{ij}(2)} \right]}} \tag{3.12}$$

is an approximation to the unobservable innovation associated with this fish and, therefore, a plot of $\{\hat{Y}_{ijk}, \tilde{S}_{ijk}; \ k = 1,\ldots,N_{ij}\}$ approximates the aforementioned desired plot.

Figure 1a shows a residual plot for North Carolina brown male shrimp using all available data. Note the points marked with circles. To the most casual observer, they suggest a behavioral pattern other than a random one. A check on these points revealed that the associated fish all were caught during the first week after release. Suspecting possible errors in recording their lengths or recapture dates, we decided to omit these samples. Figure 1b shows a more acceptable-appearing revised residual plot omitting these points.

One can also check on the approximate normality of the $\tilde{S}_{ijk}$ by plotting
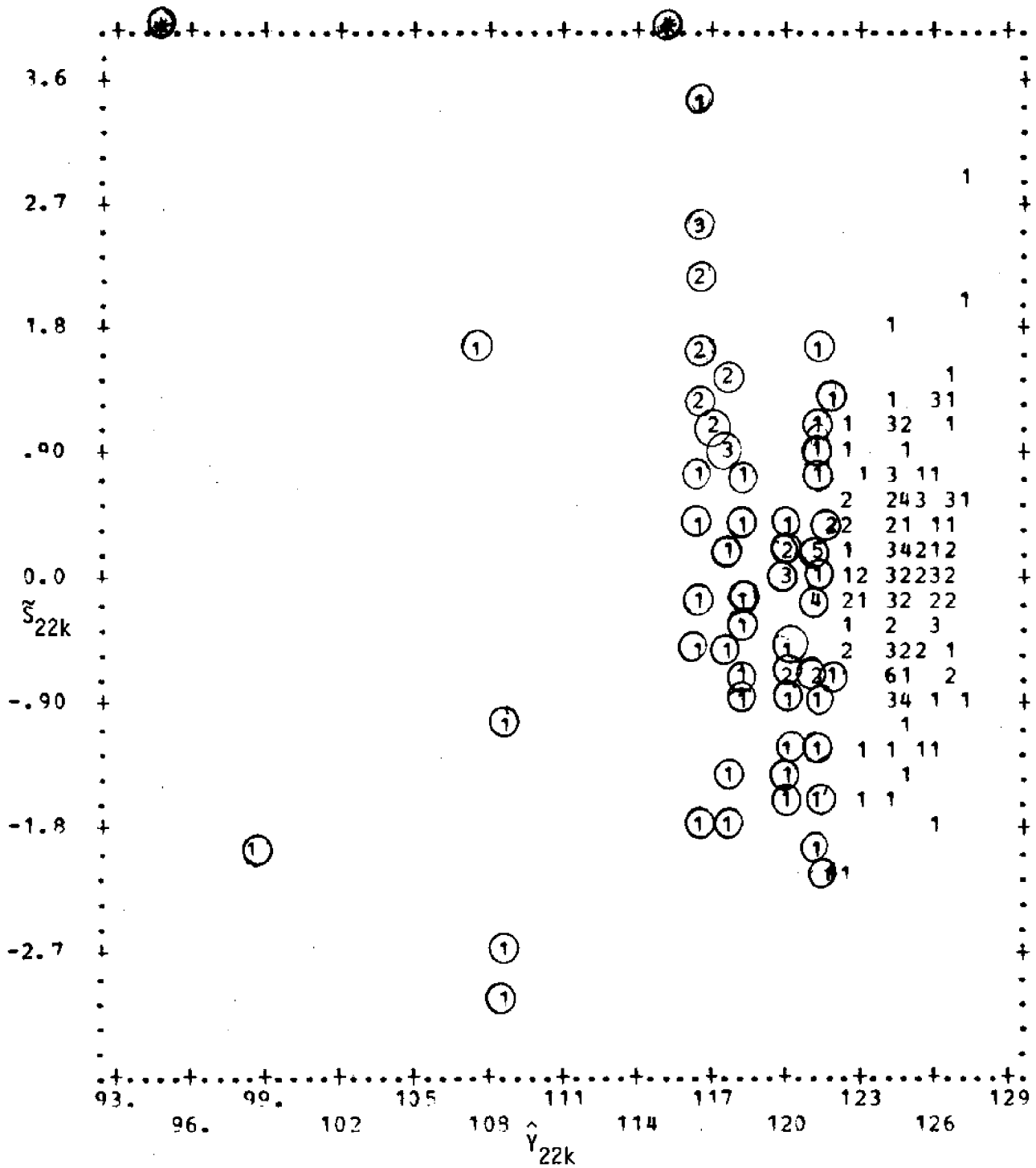
FIGURE 1a. RESIDUAL PLOT FOR NORTH CAROLINA BROWN
MALE SHRIMP GROWTH-TIME RELATIONSHIP USING
ALL DATA. Circles indicate shrimp caught
within the first week. Numbers indicate
number of points at coordinates.
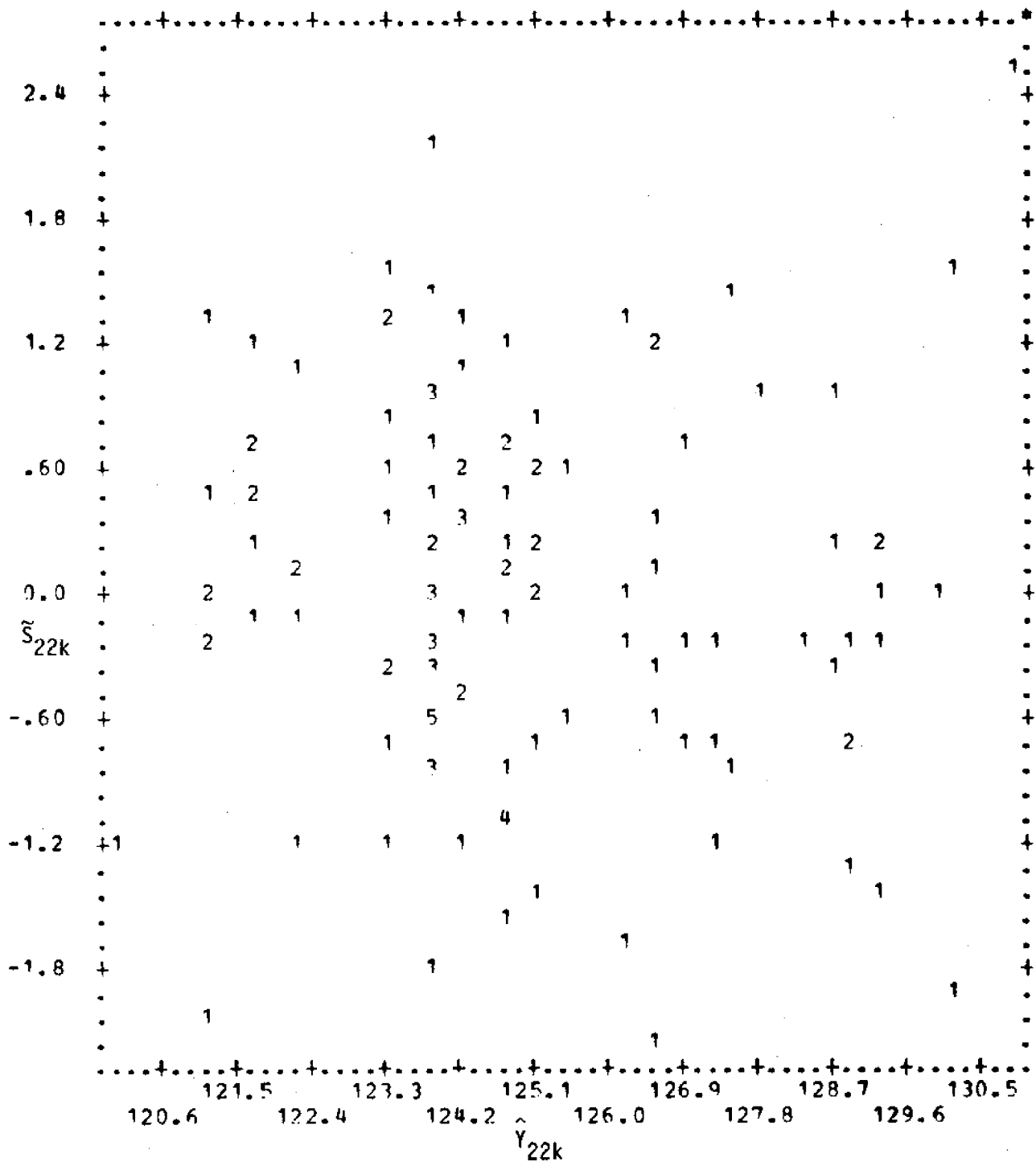
FIGURE 1b. RESIDUAL PLOT FOR NORTH CAROLINA BROWN
MALE SHRIMP GROWTH-TIME RELATIONSHIP.
SHRIMP CAUGHT IN FIRST WEEK NOT USED IN
ESTIMATION.

the empirical distribution function

$$F(s) = \frac{1}{N_{ij}} \sum_{k=1}^{N_{ij}} I_{(-\infty, s]} (\tilde{S}_{ijk}) \qquad (3.13)$$

$$I_{(-\infty, s]}(\tilde{S}_{ijk}) = \begin{cases} 0 & \tilde{S}_{ijk} > s \\ \\ 1 & \tilde{S}_{ijk} \leq s \end{cases}$$

against the cumulative normal distribution function $\Phi(s)$ where $\Phi(\cdot)$ is defined in (2.2) . A straight line supports the assumption that the innovations are normally distributed. Figure 2 shows these confirming results for North Carolina brown male shrimp.

FIGURE 2. CUMULATIVE NORMAL DISTRIBUTION FUNCTION
VERSUS EMPIRICAL DISTRIBUTION FUNCTION
FOR NORTH CAROLINA BROWN MALE SHRIMP
GROWTH-TIME RELATIONSHIP

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4. Testing for Sex and Subspecies Differences in Growth

The reader will note the apparent distinct values for $\hat{\beta}_{11}$, $\hat{\beta}_{12}$, $\hat{\beta}_{21}$ and $\hat{\beta}_{22}$ and similar differences for the $\hat{\lambda}_{ij}$'s and $\hat{\sigma}^2_{ij}$'s . Regardless of whether in reality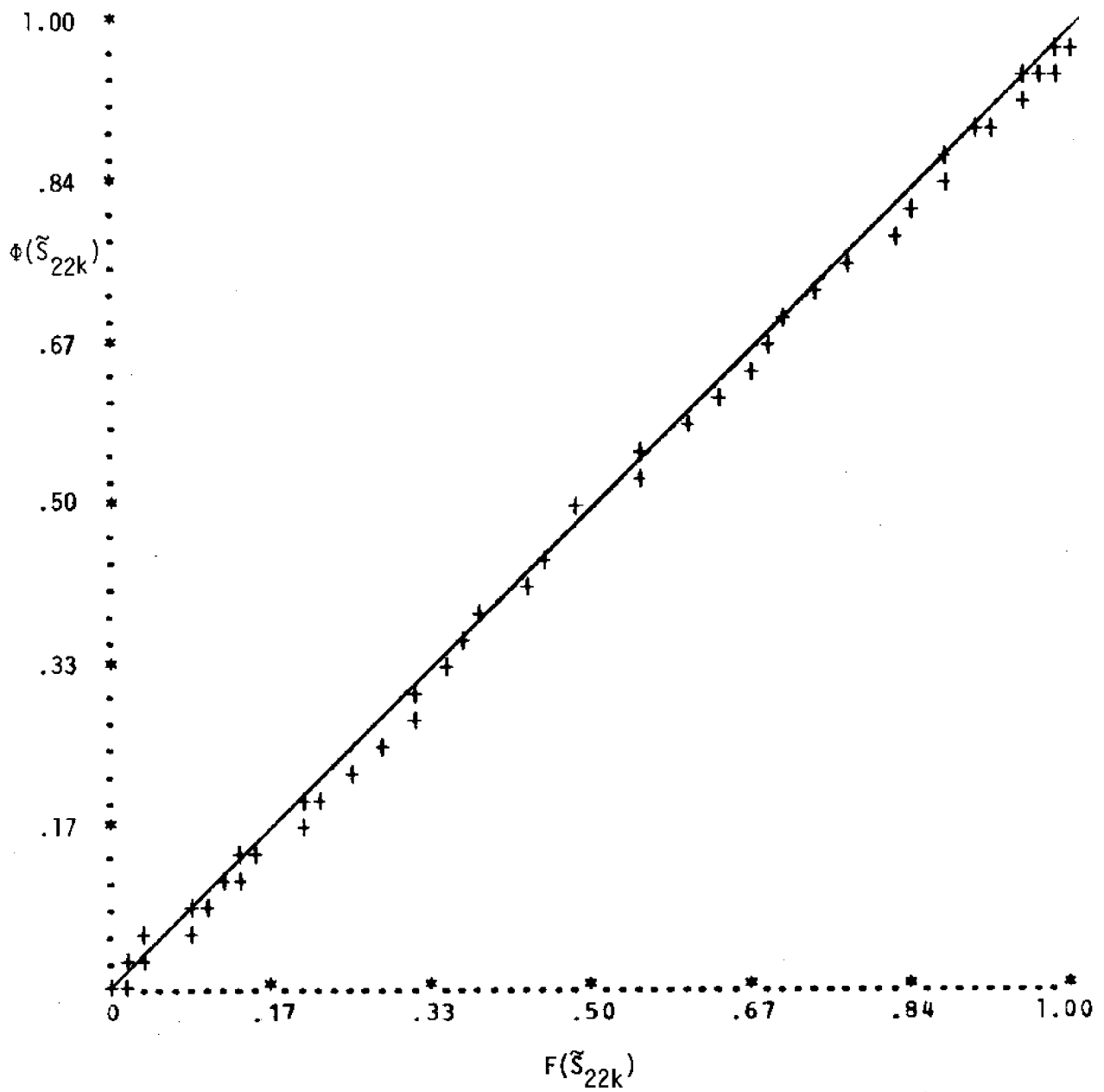 the β_{ij}'s were equal, the λ_{ij}'s equal and the σ^2_{ij}'s equal, one would expect sampling variation to produce distinct $\hat{\beta}_{ij}$'s, $\hat{\lambda}_{ij}$'s and $\hat{\sigma}^2_{ij}$'s . Since a basic principle of modeling is to reduce quantitative description to the fewest parameters necessary for adequate representation, one would like to determine if the observed differences are real or due to sampling variation. In the present setting one can use the *likelihood ratio* (to be defined shortly) to test for equalities. In particular, we begin with the null hypothesis:

H_0. Shrimp of subspecies i and sex j grow at rate β_{ij}, have mean length λ_{ij} at maturity and exhibit a degrees of variation σ^2_{ij} in length.

Initially we concentrate on three alternative hypotheses:

H_1. Shrimp of different subspecies and sex grow at the same rate $(\beta = \beta_{11} = \beta_{12} = \beta_{21} = \beta_{22})$, have the same mean length at maturity $(\lambda = \lambda_{11} = \lambda_{12} = \lambda_{21} = \lambda_{22})$ and exhibit the same variation $(\sigma^2 = \sigma^2_{11} = \sigma^2_{12} = \sigma^2_{21} = \sigma^2_{22})$.

H_2. Regardless of sex, shrimp of a given subspecies grow at the same rate $(\beta_{1.} = \beta_{11} = \beta_{12}, \quad \beta_{2.} = \beta_{21} = \beta_{22})$,

have the same mean length at maturity $(\lambda_{1.} = \lambda_{11} = \lambda_{12}$,

$\lambda_{2.} = \lambda_{21} = \lambda_{22})$, and exhibit the same variation

$(\sigma_{1.}^2 = \sigma_{11}^2 = \sigma_{12}^2, \quad \sigma_{2.}^2 = \sigma_{21}^2 = \sigma_{22}^2)$.

H_3. Regardless of subspecies, shrimp of a given sex grow at the same rate $(\beta_{.1} = \beta_{11} = \beta_{21}, \quad \beta_{.2} = \beta_{12} = \beta_{22})$, have the same mean length at maturity $(\lambda_{.1} = \lambda_{11} = \lambda_{21}$,

$\lambda_{.2} = \lambda_{12} = \lambda_{22})$ and exhibit the same variation $(\sigma_{.1}^2 = \sigma_{11}^2 = \sigma_{21}^2, \quad \sigma_{.2}^2 = \sigma_{12}^2 = \sigma_{22}^2)$.

For H_1 and $N = N_{11} + N_{12} + N_{21} + N_{22}$ one has

$$\hat{\lambda} = \frac{\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{N_{ij}} A_{ijk}(\hat{\beta})}{\sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{N_{ij}} B_{ijk}(\hat{\beta})}$$

(4.1)

$$\hat{\sigma}^2 = \frac{1 - \hat{\beta}(2)}{N} \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{N_{ij}} C_{ijk}(\hat{\beta}, \hat{\lambda}) \; ;$$

for H_2:

$$\hat{\lambda}_{i.} = \frac{\sum_{j=1}^{2} \sum_{k=1}^{N_{ij}} A_{ijk}(\hat{\beta}_{i.})}{\sum_{j=1}^{2} \sum_{k=1}^{N_{ij}} B_{ijk}(\hat{\beta}_{i.})}$$

(4.2)

$$\hat{\sigma}_{i.}^2 = \frac{1 - \hat{\beta}_{i.}(2)}{N_{i1} + N_{i2}} \sum_{j=1}^{2} \sum_{k=1}^{N_{ij}} C_{ijk}(\hat{\beta}_{i.}, \hat{\lambda}_{i.}) \qquad i = 1,2 \; ;$$

and for H_3:

$$\hat{\lambda}_{.j} = \frac{\sum\limits_{i=1}^{2} \sum\limits_{k=1}^{N_{ij}} A_{ijk}(\hat{\beta}_{.j})}{\sum\limits_{i=1}^{2} \sum\limits_{k=1}^{N_{ij}} B_{ijk}(\hat{\beta}_{.j})}$$

(4.3)

$$\hat{\sigma}^2_{.j} = \frac{1 - \hat{\beta}^2_{.j}(2)}{N_{1j} + N_{2j}} \sum\limits_{i=1}^{2} \sum\limits_{k=1}^{N_{ij}} C_{ijk}(\hat{\beta}_{.j}, \hat{\lambda}_{.j}) \qquad j = 1,2 \ .$$

Let

$$\hat{\underline{\omega}}_0 = (\hat{\beta}_{11}, \hat{\beta}_{12}, \hat{\beta}_{21}, \hat{\beta}_{22}, \hat{\lambda}_{11}, \hat{\lambda}_{12}, \hat{\lambda}_{21}, \hat{\lambda}_{22}, \hat{\sigma}^2_{11}, \hat{\sigma}^2_{12}, \hat{\sigma}^2_{21}, \hat{\sigma}^2_{22})$$

$$\hat{\underline{\omega}}_1 = (\hat{\beta}, \hat{\beta}, \hat{\beta}, \hat{\beta}, \hat{\lambda}, \hat{\lambda}, \hat{\lambda}, \hat{\lambda}, \hat{\sigma}^2, \hat{\sigma}^2, \hat{\sigma}^2, \hat{\sigma}^2)$$

(4.4)

$$\hat{\underline{\omega}}_2 = (\hat{\beta}_{1.}, \hat{\beta}_{1.}, \hat{\beta}_{2.}, \hat{\beta}_{2.}, \hat{\lambda}_{1.}, \hat{\lambda}_{1.}, \hat{\lambda}_{2.}, \hat{\lambda}_{2.}, \hat{\sigma}^2_{1.}, \hat{\sigma}^2_{1.}, \hat{\sigma}^2_{2.}, \hat{\sigma}^2_{2.})$$

$$\hat{\underline{\omega}}_3 = (\hat{\beta}_{.1}, \hat{\beta}_{.2}, \hat{\beta}_{.1}, \hat{\beta}_{.2}, \hat{\lambda}_{.1}, \hat{\lambda}_{.2}, \hat{\lambda}_{.1}, \hat{\lambda}_{.2}, \hat{\sigma}^2_{.1}, \hat{\sigma}^2_{.2}, \hat{\sigma}^2_{.1}, \hat{\sigma}^2_{.2}) \ .$$

To test H_0 versus H_k for $k > 0$, one uses the likelihood ratio $R_k = h(\hat{\underline{\omega}}_k)/h(\hat{\underline{\omega}}_0)$. If H_k is true, then it is known that as N_{11}, N_{12}, N_{21} and N_{22} increase, the quantity $-2 \ln R_k$ has a chi-squared distribution with 9, 6, and 6 degrees of freedom for $k = 1, 2$ and 3 respectively. Let X be a chi-squared random variable with f degrees of freedom and define

$$P_k = pr(X \geq -2 \ln R_k | H_k \text{ is true}) \quad .$$

Here P_k is the *P-value* associated with hypothesis H_k and is a measure of its credibility. For example, one inclines to accept a hypothesis whose P-value, say, exceeds 0.05 but is reluctant to place much confidence in an hypothesis whose P-value is less than, say, 0.01 .

Table 5 gives $-2 \ln R_k$ and P_k for hypotheses 1, 2 and 3 . Here a low P-value encourages us to reject hypothesis 1, that no differences exist with regard to subspecies and sex. Note that the P-value for hypothesis 2 encourages us to reject the hypothesis that sex does not matter. Similarly, we reject hypothesis 3 that subspecies does not matter.

Table 5
Likelihood Ratio Tests for
North Carolina Pink and Brown Shrimp Growth Parameters

k	Hypothesis	$-2 \ln R_k$	P_k
1.	Subspecies and Sex Do Not Matter	377.52	< .0001
2.	Sex Does Not Matter	278.40	< .0001
3.	Subspecies Does Not Matter	120.06	< .0001

5. Weight-Length Relationship

Studies of the weight-length relationship in fish customarily use the model

$$W = aL^b \qquad\qquad 0 < a,b \qquad\qquad (5.1)$$

where W denotes weight and L denotes length. Here we consider a more complete quantitative description

$$W = aL^b \varepsilon \qquad\qquad\qquad (5.2)$$

where $\eta = \ln \varepsilon$ is a normally distributed random variable with mean zero and variance γ^2. To estimate a, b and γ^2, one uses the *linearized* model

$$\ln W = \tilde{a} + b \ln L + \eta$$
$$\tilde{a} = \ln a \qquad . \qquad\qquad\qquad (5.3)$$

In practice, one may apply the linear least-squares regression method to (5.3) using a sample of weight-length data for each subspecies and sex. The resulting estimates for the shrimp data appear in Table 6 . Since η is normal, these least-squares estimates are identical to those attainable through the maximum likelihood method except for a minor adjustment to the estimate of γ^2 . Therefore, they have all the desirable statistical properties mentioned in earlier sections.

Goodness-of-Fit for Weight-Length Model

As in the case of the growth curve, one would like to check the extent

Table 6

Maximum Likelihood Estimates for the
Weight-Length Relationship
for North Carolina Pink and Brown Shrimp[a]

Shrimp		i	j	N_{ij}	$\hat{\tilde{a}}_{ij}$	$\hat{a}_{ij}$	$\hat{b}_{ij}$	$\hat{\gamma}^2_{ij}$
Pink	Female	1	1	242	-11.94	6.664×10^{-6}	3.078	.00386
	Male	1	2	277	-11.74	8.152×10^{-6}	3.021	.00359
Brown	Female	1	1	239	-12.17	5.250×10^{-6}	3.109	.00343
	Male	1	2	261	-11.99	6.284×10^{-6}	3.066	.00307

$$a\hat{\gamma}^2_{ij} = \frac{N_{ij} - 2}{N_{ij}} \times \text{least-squares estimate of } \gamma^2_{ij} .$$

to which the form in (5.3) applies and the extent to which normality applies. Although the random term η is not observable for each fish, one can approximate it for fish k of subspecies i and sex j by the residual

$$\hat{\eta}_{ijk} = \ln W_{ijk} - \hat{\tilde{a}}_{ij} - \hat{b}_{ij} \ln L_{ijk} \quad . \tag{5.4}$$

Let $\ln \widehat{W}_{ijk} = \hat{\tilde{a}}_{ij} + \hat{b}_{ij} \ln L_{ijk}$ and $\tilde{\eta}_{ijk} = \hat{\eta}_{ijk}/\hat{\gamma}_{ij}$. In contrast to Section 3 , one expects the residuals to have a relatively constant variance for large N_{ij} . However, as before one expects a plot of $\{\tilde{\eta}_{ijk}, \ln \widehat{W}_{ijk};$ $k = 1,\ldots,N_{ij}\}$ to reveal no association. Since high correlation can occur between $\ln W_{ijk}$ and $\ln L_{ijk}$ even when $\tilde{\eta}_{ijk}$ and $\ln \widehat{W}_{ijk}$ show association, the correlation coefficient is not a sufficiently comprehensive measure of goodness-of-fit for present purposes. Figure 3 shows an example of this plot for pink female shrimp. No pattern appears here, nor do any appear for pink male, brown female
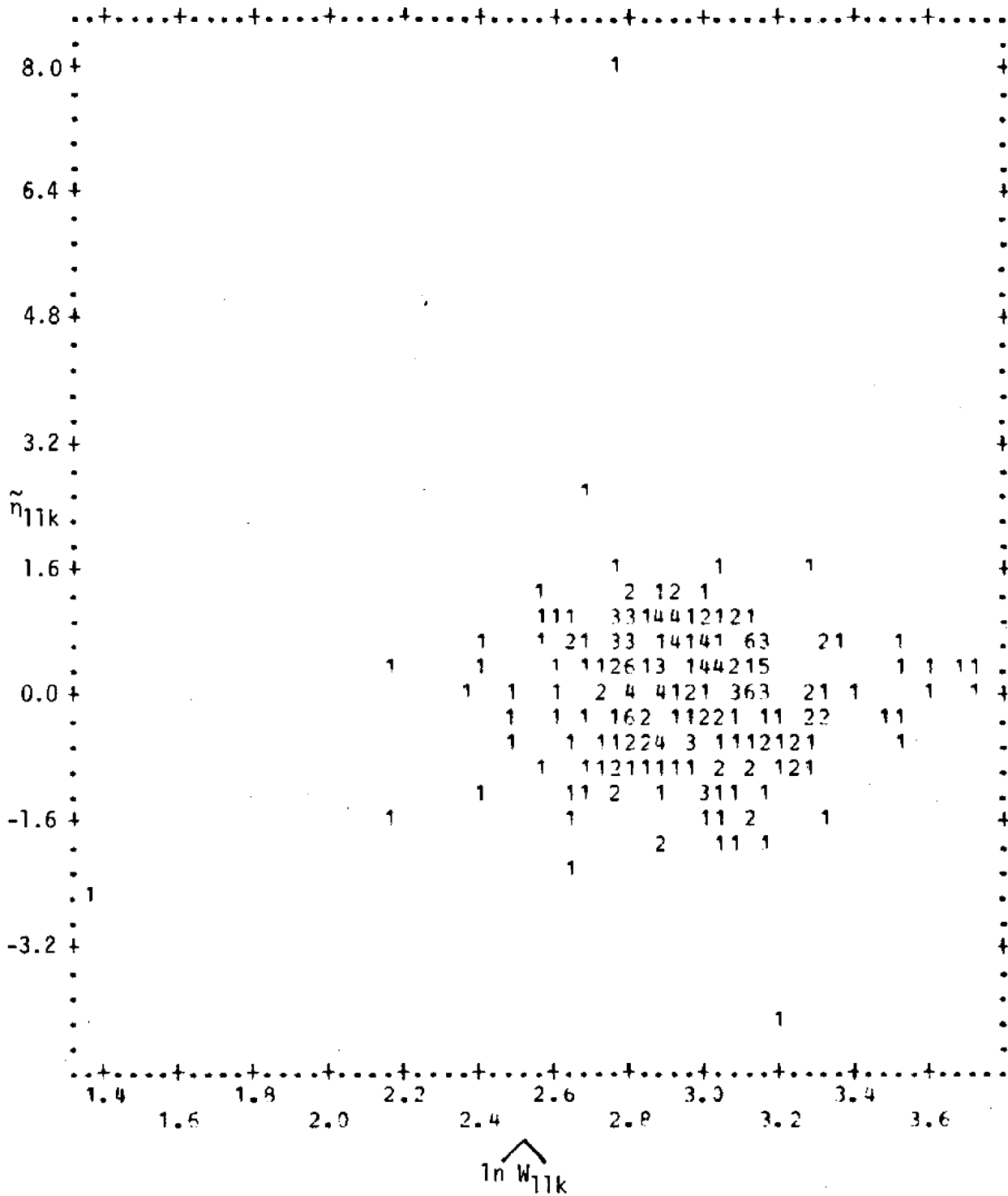
FIGURE 3.   RESIDUAL PLOT FOR NORTH CAROLINA PINK FEMALE
SHRIMP WEIGHT-LENGTH RELATIONSHIP

or brown male shrimp.

To check for normality the empirical cumulative distribution function

$$F_{ij}(s) = \frac{1}{N_{ij}} \sum_{k=1}^{N_{ij}} I_{(-\infty, s]}(\tilde{n}_{ijk}) \tag{5.5}$$

can be plotted versus $\Phi(s)$. Figure 4 shows $\{F_{ij}(\tilde{n}_{ijk}), \Phi(\tilde{n}_{ijk});$ $k = 1, \ldots, N_{ij}\}$ for pink female $(i = 1, j = 1)$ shrimp. The relative straight line is encouraging evidence of normality. The plots for pink male, brown female and brown male shrimp are also relatively linear, offering additional evidence of normality.

FIGURE 4. CUMULATIVE NORMAL DISTRIBUTION FUNCTION
VERSUS EMPIRICAL DISTRIBUTION FUNCTION
FOR NORTH CAROLINA PINK FEMALE SHRIMP
WEIGHT-LENGTH RELATIONSHIP

6. Testing for Sex and Subspecies Difference In the Weight-Length Relationship

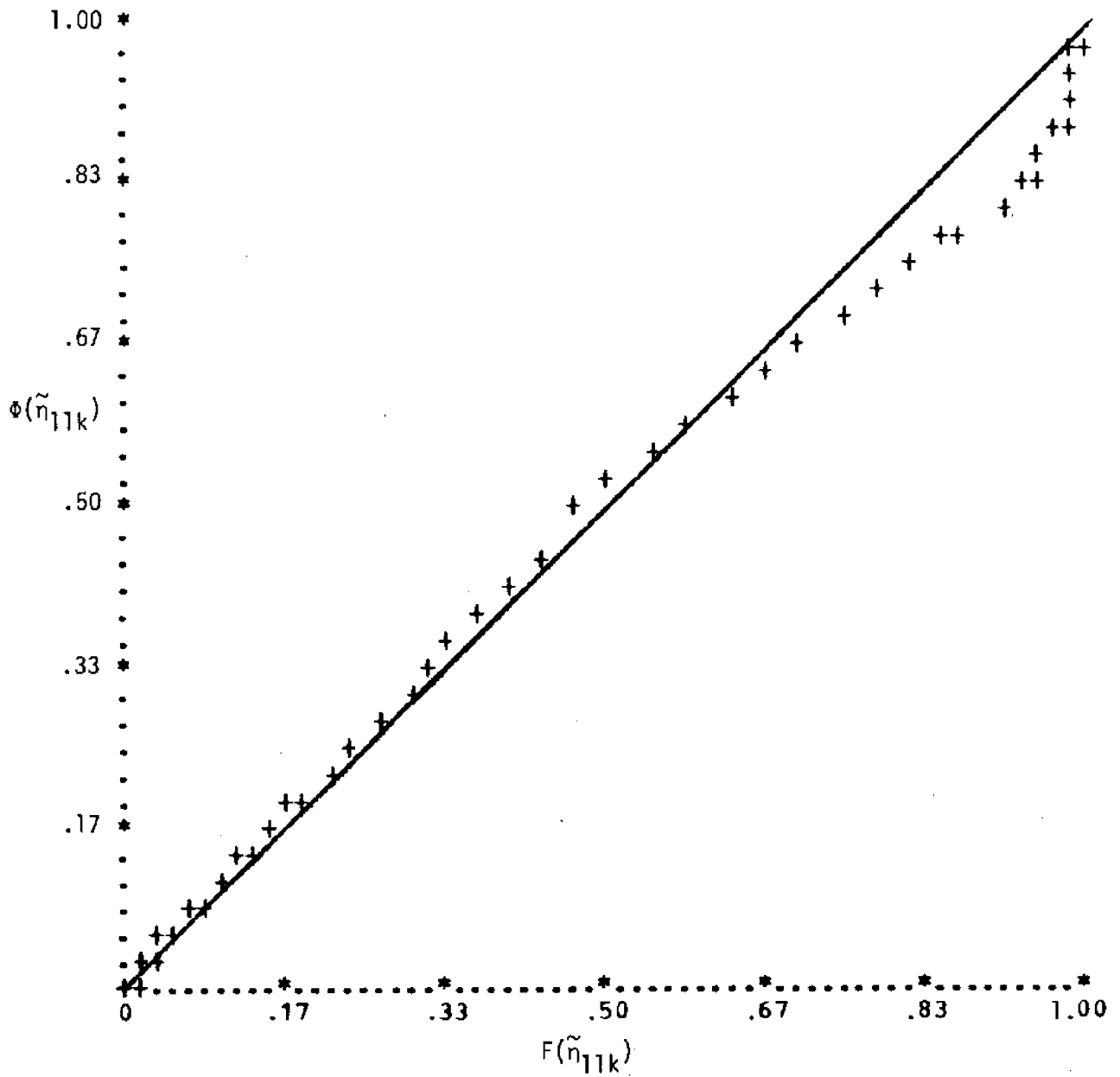As in the case of growth, it is a desirable objective to reduce the number of parameters $\{a_{ij}, b_{ij}, \gamma_{ij}^2, \; i,j = 1,2\}$ to a smaller subset. In particular, doing so enables one to identify similarities across subspecies and sex when they exist. Again we consider four hypotheses:

H_0. Shrimp of subspecies i and sex j have parameters a_{ij}, b_{ij} and γ_{ij}^2 .

H_1. Neither subspecies nor sex affects the weight-length relationship: $a = a_{11} = a_{12} = a_{21} = a_{22}$, $b = b_{11} = b_{12} = b_{21} = b_{22}$, $\gamma^2 = \gamma_{11}^2 = \gamma_{12}^2 = \gamma_{21}^2 = \gamma_{22}^2$.

H_2. Sex does not affect the weight-length relationship:
$a_{1.} = a_{11} = a_{12}$, $a_{2.} = a_{21} = a_{22}$, $b_{1.} = b_{11} = b_{12}$, $b_{2.} = b_{21} = b_{22}$, $\gamma_{1.}^2 = \gamma_{11}^2 = \gamma_{12}^2$, $\gamma_{2.}^2 = \gamma_{21}^2 = \gamma_{22}^2$.

H_3. Subspecies does not affect the weight-length relationship:
$a_{.1} = a_{11} = a_{21}$, $a_{.2} = a_{12} = a_{22}$, $b_{.1} = b_{11} = b_{21}$, $b_{.2} = b_{12} = b_{22}$, $\gamma_{.1}^2 = \gamma_{11}^2 = \gamma_{21}^2$, $\gamma_{.2}^2 = \gamma_{12}^2 = \gamma_{22}^2$.

Fortunately, estimates of these quantities under each hypothesis are easily obtained by a standard linear least-squares computer package such as BMD (1975) or SAS (1976) . Let a circumflex over a quantity denote an estimate. Moreover, one can show that R_k , the likelihood ratio of H_k

versus H_0 , simplifies to

$$R_1 = \left[\frac{(\hat{\gamma}^2)^N}{\prod\limits_{i=1}^{2} \prod\limits_{j=1}^{2} (\hat{\gamma}_{ij})^{N_{ij}}} \right]^{-\frac{1}{2}} \qquad N = N_{11} + N_{12} + N_{21} + N_{22} \qquad (6.1a)$$

$$R_2 = \left[\frac{\prod\limits_{i=1}^{2} (\hat{\gamma}_{i.}^2)^{N_{i1}+N_{i2}}}{\prod\limits_{i=1}^{2} \prod\limits_{j=1}^{2} (\hat{\gamma}_{ij}^2)^{N_{ij}}} \right]^{-\frac{1}{2}} \qquad (6.1b)$$

$$R_3 = \left[\frac{\prod\limits_{j=1}^{2} (\hat{\gamma}_{.j}^2)^{N_{1j}+N_{2j}}}{\prod\limits_{i=1}^{2} \prod\limits_{j=1}^{2} (\hat{\gamma}_{ij}^2)^{N_{ij}}} \right]^{-\frac{1}{2}} \qquad \cdot \qquad (6.1c)$$

Under H_k , $-2 \ln R_k$ asymptotically has a chi-squared distribution with 9, 6 and 6 degrees of freedom respectively. Table 7 presents the results of hypothesis testing, which tend to favor H_0: the weight-length relationship is heterogeneous across subspecies and sex.

Table 7
Hypothesis Testing for
Weight-Length Relationship

k	Hypothesis	$-2 \ln R_k$	P-Value
1.	Subspecies and Sex Do Not Matter	638.19	< .0001
2.	Sex Does Not Matter	454.03	< .0001
3.	Subspecies Does Not Matter	174.31	< .0001

7. Distribution of Biomass

Although the growth-time and weight-length relationships of earlier sections provide useful characterizations of individual North Carolina shrimp, more often than not interest focuses on aggregate descriptors such as biomass. In addition to the aforementioned growth and weight-length descriptors, biomass depends on recruitment, mortality, migratory patterns and fishing intensity, at a minimum. Although the current report in no way addresses these factors, we can show how knowledge of the growth curves and weight-length relationship allows us to describe the distribution of biomass of a population of N mature shrimp. A later report will extend this development to the case of constant recruitment at varying intensities where all shrimp are not mature.

We begin our discussion by computing the mean and variance of weight of an individual mature shrimp. Recall from Section 2 that a mature shrimp has a normally distributed length with mean λ and variance $\sigma_L^2 = \sigma^2/(1-\beta^2)$. Also recall from Section 5 that weight and length are related by

$$W = aL^b\eta \tag{7.1}$$

where a and b are constants and $\ln \eta$ is a normal variate with mean zero and variance γ^2 . Then weight has mean

$$E(W) = aE(L^b)E(\eta) \tag{7.2}$$

and variance

$$\text{var}(W) = a^2[E(L^{2b})E(\eta^2) - E^2(L^b)E^2(\eta)] \quad . \tag{7.3}$$

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Now

$$E(\eta) = e^{\gamma^2/2} \qquad\qquad E(\eta^2) = e^{2\gamma^2} \quad, \tag{7.4}$$

as a consequence of the normality of $\ln \eta$. Moreover, the normality of L enables one to write for $\sigma_L/\lambda \ll 1$ and noninteger c

$$E(L^c) \approx \lambda^c + q_k(c) \tag{7.5}$$

where

$$q_k(c) = \sum_{i=1}^{k} g_{2i}(c)\mu_{2i} \tag{7.6a}$$

$$g_i(c) = g_{i-1}(c) \frac{\sigma_L(c-i+1)}{\lambda i} \qquad\qquad g_0(c) = \lambda^c \tag{7.6b}$$

and μ_i is the ith moment of a normal random variable from $N(0,1)$. For example, k = 6, which approximates well in practice, leads to

$$\mu_2 = 1, \qquad \mu_4 = 3, \qquad \mu_6 = 15$$
$$\tag{7.7}$$
$$\mu_8 = 105, \qquad \mu_{10} = 945 \qquad \mu_{12} = 10395 \quad.$$

Then one has

$$E(W) \approx ae^{\gamma^2/2}[\lambda^b + q_k(b)] \tag{7.8}$$

$$var(W) \approx a^2 e^{\gamma^2}\{e^{\gamma^2}[\lambda^{2b} + h_k(2b)] - [\lambda^b + q_k(b)]^2\} \quad. \tag{7.9}$$

37

The $\approx$ symbol serves to remind the reader of the approximating nature of the result. In general, estimates of b will be nonintegral. Rounding b to an integer can lead to serious error.

Although the weight of an individual fish is not normally distributed, the biomass of N fish, where N is large, has a normal distribution with mean $N E(W)$ and variance $N \text{var}(W)$. Let the subscripts i and j denote subspecies i and sex j and suppose that the proportion of fish of subspecies i and sex j in a population of N fish is p_{ij} for $i,j = 1,2$ so that $p_{11} + p_{12} + p_{21} + p_{22} = 1$. Then the biomass B_N for large N has a normal distribution with mean

$$E(B_N) \approx N \sum_{i,j=1}^{2} p_{ij} a_{ij} e^{\gamma_{ij}^2/2} [\lambda_{ij}^{b_{ij}} + q_k(b_{ij})] \qquad (7.10)$$

and variance

$$\text{var}(B_N) \approx N \left\{ \sum_{i,j=1}^{2} p_{ij} a_{ij}^2 e^{2\gamma_{ij}^2} \left[\lambda_{ij}^{2b_{ij}} + q_k(2b_{ij}) \right] \right.$$
$$\left. - \left[\sum_{i,j=1}^{2} p_{ij} a_{ij} e^{\gamma_{ij}^2/2} \left[\lambda_{ij}^{b_{ij}} + q_k(b_{ij}) \right] \right]^2 \right\} . \qquad (7.11)$$

The reader should regard (7.10) and (7.11) as the illustration of a concept. In an observable population, not all fish are of the same age. Therefore, the characteristics (mean, variance and distribution) depend on the proportions of fish of different ages. Expressions (7.10) and (7.11) can be modified when these proportions are known. We do this in a subsequent paper when tracing the migratory pattern of North Carolina shrimp.

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of Canada.

9. Definition of Terms

Term	Definition	
a	Parameter in weight-length relationship.	1
$\tilde{a}$	ln a .	28
$A_{ijk}(\hat{\beta})$	Function used in maximum likelihood estimation of growth parameters.	15
b	Parameter in weight-length relationship.	1
$B_{ijk}(\hat{\beta})$	Function used in maximum likelihood estimation of growth parameters.	15
B_N	Biomass of N fish.	38
$C_{ijk}(\hat{\beta}, \hat{\lambda})$	Function used in maximum likelihood estimation of growth parameters.	15
$e(\cdot)$	Error function.	9
$E(\cdot)$	Expected value operator.	36
$ERF(\cdot)$	Fortran error function.	9
$g(\cdot)$	Normal density with mean $\lambda(1-\beta^Z) - X\beta^Z$ and variance $\dfrac{\sigma^2 (1 - \beta^{2z})}{1 - \beta^2}$.	13
$g_i(c)$	Recursive function used in calculating $q(c)$.	37
$G_0(\cdot)$	Distribution of length of mature shrimp.	4
$G_4(\cdot)$	Distribution of length of a shrimp at time t given length L at time t_0 .	4
$G_8(\cdot)$	Distribution of length of a shrimp at time t given length L at time t_0 is normally distributed with mean $\mu(L)$ and variance $\sigma^2(L)$.	5
$\tilde{G}_i(\cdot)$	Mixture distribution of the distributions $G_{i1}(\cdot)$ and $G_{j1}(\cdot)$.	7
$G_{ij}(\cdot)$	Distribution i for sex j ($i = 0,4,8$) .	5
$h(\underline{\omega})$	Likelihood function for growth parameter estimation.	13

Term	Definition	Page of First Mention
$I_{(x,y]}(\cdot)$	Indicator function.	22
K	Instantaneous growth rate.	1
L	Length.	1
$\tilde{L}$	Temporary storage used in algorithms.	$Q(p,L^*,\delta)$ - 12 MLEG - 16
L_t	Length at time t.	1
L_∞	Mean length at maturity.	1
$m(\underline{\omega})$	$\ln h(\underline{\omega})$.	14
N	Number in sample.	13
$N(\mu, 1)$	Normal distribution with mean μ and variance unity.	37
$q(\cdot)$	Function used in Taylor expansion of $E(L^c)$.	37
$q_k(\cdot)$	Function used in Taylor expansion of $E(L^c)$.	37
$Q_i(p)$	pth quantile for the distribution $G_i(\cdot)$.	10
R_k	Likelihood ratio for hypothesis k.	26
S_{ijk}	Residual length for fish k.	19
$\tilde{S}_{ijk}$	Normalized residual length for fish k.	19
$\tilde{U}$	Temporary storage used in algorithms.	$Q(p,L^*,\delta)$ - 12 MLEG - 16
U_t	Normally distributed random variable with mean 0 and variance σ^2.	3
V_t	Linear combination of U_t s.	3
W	Weight.	1
X	Length of a shrimp at time of release in a mark recapture study.	13
Y	Length of a shrimp at time of recapture.	13
Z	Time interval between release and recapture.	13

Term	Definition	Page of First Mention
α	$L_\infty(1 - \beta)$.	3
β	e^{-K} .	3
$\beta(z)$	β^z .	13
γ^2	Variance of η .	28
δ	Accuracy parameter for algorithm MLEG.	17
ε	Lognormally distributed random variable.	28
η	Normally distributed random variable with mean 0 and variance γ^2 .	28
λ	Mean length at maturity (see L_∞) .	3
$\mu(L)$	Mean length at time t_0 .	5
μ_i	ith moment of a standard normal random variable.	37
$\mu_t(t_0)$	Mean length at time t given $\mu(L)$ and $\sigma^2(L)$.	5
$\mu_t(L, t_0)$	Mean length at time t given length L at time t_0 .	4
ρ	Probability that a shrimp from the sampled population is female.	7
$\sigma^2(L)$	Variance of length at time t_0 .	5
$\sigma_t^2(t_0)$	Variance of length at time t given $\mu(L)$ and $\sigma^2(L)$.	5
$\sigma_t^2(L, t_0)$	Variance of length at time t given length L at time t_0 .	4
$\phi(\cdot)$	Standard normal density.	3
$\underline{\omega}_{ij}$	Vector of growth parameters.	13

Note:

(i) Unless otherwise indicated, all subscripts i, j, k are interpreted as i: subspecies, j: sex, k: individual .

(ii) Any parameter with $\wedge$ above it is an estimate of that parameter.