

**Abstract.**—An alternative approach, Central Location Measure, to estimating the growth parameters from length-frequency data was proposed and applied to green tiger prawns, *Penaeus semisulcatus*, from Kuwait waters. The proposed method estimates mean length at age by defining a central location around the mode of the length-frequency distribution for a cohort and then estimates the growth parameters by using the method of the nonlinear least squares. The variances and covariances for the growth parameters derived from the nonlinear-fitting technique enable statistical comparisons of growth performance between sexes, cohorts, or populations. Bootstrap simulations indicated that the proposed method was satisfactory in estimating the growth parameters for green tiger prawns, and that, therefore, it may be applied to other short-lived crustacean species with discontinuous recruitment. Significant differences in growth between male and female green tiger prawns in Kuwait waters were detected by using a multivariate test ( $P < 0.005$ ), and annual variations in growth were more obvious in males than in females, indicating that growth of males may be more vulnerable to environmental changes.

## An alternative approach to estimating growth parameters from length-frequency data, with application to green tiger prawns

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Growth parameters for crustacean populations are usually estimated from length-frequency data because of the lack of reliable methods for ageing decapods. Pauly and David (1980) integrated Petersen's method (Petersen, 1891) and Modal Class Progression Analysis (George and Banerji, 1964) into a single approach named ELEFAN I, which has been implemented in the computer software of Compleat ELEFAN (Pauly, 1987; Gayanilo et al., 1989). It has been widely applied in growth studies, especially in the tropical and subtropical areas. Shepherd (1987) proposed the SLCA method which performs a similar analysis to ELEFAN I in that both methods estimate the growth parameters by detecting the peaks and troughs in the length-frequency data; SLCA, however, applies a different goodness-of-fit function in model estimation (Holden and Bravinton, 1992). Harding (1949), Cassie (1954), Tanaka (1956), Hasselblad (1966), Bhattacharya (1967), MacDonald and Pitcher (1979), and Sparre (1987a) developed methods for analysis of length-frequency distributions based on the normal distribution assumption of the length-frequency for each cohort. McNew and Summerfelt (1978) discussed the case when the length distribution at each age was not normal. Some

computer programs (Abramson, 1971; Young and Skillman, 1975; Sparre, 1987b; Sparre et al., 1989) were developed for implementing these parametric methods. A difficulty in applying probability distributions to separate each age group is that the breaking points between age groups can be quite ambiguous owing to the problems of overlapping distributions. Schnute and Fournier (1980) proposed an approach using biological structure as constraints to eliminate the ambiguity.

All the above methods are based on information on the central location of the length-frequency data. There are many ways to measure the central location of a distribution, such as the mode if the distribution is symmetric, the median, the mean, and the trimmed mean. The mean is sensitive to outlying values in a sample, whereas the mode and median are insensitive to these outliers. The trimmed mean is a compromise between the mean and median in the sensitivity to outliers (Devore, 1987) and might be preferred in order to obtain a representative location of the length distribution of an animal by a sample. For a species with multiple overlapping cohorts in length distribution, however, it is impossible to estimate the mean, median, and trimmed mean without an assump-

tion of the mixture of the components in the distribution. Following the idea of the trimmed mean and the idea of the mode, one is able to define a central location which is located around the mode with a certain amount of spread. A central value can be estimated from this spread and used to represent the mean length for the cohort at time  $i$ . The estimated mean length from several length intervals around the mode should be more robust than the mode in representing the growth of a cohort, especially when the length distribution is skewed, which is often the case for small-size samples. In this study, an approach using the mean length, estimated from the central part of the distribution, for estimating the parameters of a seasonal von Bertalanffy growth equation was proposed and applied to green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters. With the proposed method, which might be termed the Central Location Measure, one is able to apply the methods of the linear or nonlinear least squares in order to estimate the growth parameters with variances and covariances and thus to study the statistical differences in growth performance between sexes and between cohorts.

## Materials and methods

### The seasonal growth model and the fitting technique

Various versions of the seasonal growth models which incorporate some parameters defined by season into the von Bertalanffy model (von Bertalanffy, 1938) have been proposed (Ursin, 1963; Pitcher and MacDonald, 1973; Cloern and Nichols, 1978; Pauly and Gaschütz<sup>1</sup>). Among these models, Pauly-Gaschütz's model is the most widely used:

$$L_t = L_\infty \left\{ 1 - \exp \left[ -K \left( t - t_0 + \frac{C}{2\pi} \sin 2\pi(t - t_0) \right) \right] \right\} \quad (1)$$

where  $L_t$  = the length at age  $t$ ;  $L_\infty$  is the asymptotic length;  $K$  = the intrinsic growth rate;  $t_0$  = the age at which the length of the animal is 0; and  $t_s$  and  $C$  are the parameters defining the seasonal growth patterns.

The seasonal growth model (Eq. 1) was fitted by using the nonlinear least squares method with SAS

Proc NLIN (SAS, 1992). A SAS program for fitting the seasonal growth model with the method of the nonlinear least squares is available upon request. A multivariate test, Hotelling's  $T^2$  statistic (Johnson and Wichern, 1992), was used to test the hypothesis of no differences in growth between two populations, i.e.  $H_0: \beta_1 = \beta_2$ , if the assumption of the equality of the two covariance matrices holds; otherwise, an alternative statistic,  $T_v^2$ , for unequal covariance case (Johnson and Wichern, 1992; Hanumara and Hoenig, 1987) was used:

$$T_v^2 = (\hat{\beta}_1 - \hat{\beta}_2)' (D_1 + D_2)^{-1} (\hat{\beta}_1 - \hat{\beta}_2), \quad (2)$$

where  $\hat{\beta}$  and  $D_i$  = the vectors of the estimated growth parameters and the estimated covariance matrix of the growth parameters, respectively, for population  $i$ . The null hypothesis,  $H_0: \beta_1 = \beta_2$ , is rejected if  $T_v^2 \geq \chi_{\alpha, p}^2$ , where  $p$  is the dimension of multinormal populations. The hypothesis of equality of  $m$  covariance matrices,  $H_0: \Sigma_1 = \Sigma_2 = \dots = \Sigma_m$ , was tested by using an approximate chi-squared statistic  $MC^{-1}$  modified from Morrison (1990, p. 297), for which

$$M = \sum_{i=1}^m (n_i - 1) \ln |S| - \sum_{i=1}^m (n_i - 1) \ln |S_i|$$

and

$$C^{-1} = 1 - \frac{2p^2 + 3p - 1}{6(p + 1)(m - 1)} \left( \sum_{i=1}^m \frac{1}{n_i - 1} - \frac{m}{\sum_{i=1}^m (n_i - 1)} \right),$$

where  $n_i$  is the sample size for population  $i$ ;  $\ln$  indicates natural logarithm;  $S_i$  (the estimate of  $\Sigma_i$ ) is set as  $S_i = n_i D_i$  in this study as suggested by Hanumara and Hoenig (1987);  $S$  is the pooled estimate of the common covariance matrix of the estimated growth parameters; and  $|S|$  represents the determinant of the matrix  $S$ .

Bernard (1981) and Hanumara and Hoenig (1987) discussed the application of Hotelling's  $T^2$  in comparing the growth of fish; however, the statistics proposed by Bernard (1981) and Hanumara and Hoenig (1987) were different by a constant multiple, because they treated the covariance matrix of the growth parameters differently. In this study, the estimated covariance matrix of the growth parameters has the same form as that proposed by Hanumara and Hoenig (1987), therefore the latter was used.

### The approach to obtaining length-at-age data

To estimate the parameters in model 1 (Eq. 1), one needs a set of length-at-age data. The method pro-

<sup>1</sup> Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. Int. Coun. Explor. Sea, Council Meeting 1979/G:24, 26 p.

posed in this study to obtain length-at-age data includes the following steps: 1) arrange the monthly length-frequency samples in sequential order (the data series should begin with the month in which the new recruitment is first detected); 2) identify the mode representing the newly recruited cohort in the length-frequency distribution of the first month (this should be the smallest in size in the length distribution); 3) follow the movement of this mode from month to month to find its location in the time series; 4) define the width of the central location spreading from the mode in each month; 5) use the length data in the range of the central location to calculate the mean length weighted by the frequencies (this mean length is considered to be the mean length at month  $i$ ); and 6) according to the information on the spawning season, define the birth-month,  $a$ , for the cohort (then the age for that cohort in month  $i$  can be estimated by  $age = i - a$ ). A length-at-age data set is then established. Like that in other length-frequency analysis methods such as ELEFAN I (Pauly et al., 1984), age here should be considered relative age instead of true age. One might be able to adjust it if information on the observed spawning season for each year was available. The change of relative age, however, would only change the location but not the shape of the growth curve. Note that step 3 might be difficult for a long-lived species with highly overlapping cohorts at old ages or for species with continuous recruitment and thus result in multiple peaks in the length-frequency distribution (Brothers, 1979). For a species with distinct modes and discontinuous recruitment in one year, like green tiger prawns in Kuwait waters, the modal progression of a cohort can be easily followed from month to month. This will be shown below. Step 4 involves making subjective decisions regarding the width of the central location. If the length distribution is fairly symmetric around the mode and the cohorts in the length distribution do not highly overlap, the estimates of growth parameters should not be sensitive to the subjective selection of the width. The overlap index proposed by McNew and Summerfelt (1978) can be applied as a guideline to define the degree of overlap among the adjacent age-class distributions. The Central Location Measure should work like the trimmed mean for a single cohort case.

### Data collection

In order to obtain a series of monthly length-frequency samples that are representative of the population, monthly research vessel surveys were carried out from May 1986 to July 1990 in Kuwait waters with RV *Bahith*, a stern trawler (679 tons in gross tonnage) of the Kuwait Institute for Scientific Re-

search. Surveys were interrupted in June 1986 and December 1988 because of logistical problems. Each monthly survey included 7 to 10 fixed stations in Kuwait waters and each tow lasted from 30 to 50 min. All shrimp were sorted and weighed prior to examination of the entire catch (or a 3- to 6-kg subsample) to determine species composition and length frequencies. Carapace length, rear margin of the orbit to the posterior edge of the carapace (Dall et al., 1990), was measured to the nearest 1 mm.

Kuwait waters were partitioned into three areas (Kuwait Bay, Middle Area, and Southern Area) on the basis of species distribution and geographical considerations (Xu et al., 1995). The relative size ratios of the three areas of Kuwait Bay: Middle Area: Southern Area were 3: 4: 5, respectively. These ratios were used as weighting factors in the compilation of monthly length frequencies from the data of each sampled station.

## Results

### Length at age

The monthly carapace length (CL) frequency showed distinct modes and clear modal progression for the 1986, 1987, 1988, and 1989 spring cohorts of male and female green tiger prawns. The central location of the length distribution in each month was defined by spreading the distribution from the mode up and down for 2–3 mm. Tables 1 and 2 provide part of the monthly length-frequency data for male and female shrimp, respectively, to show the central locations (bold numbers) used to calculate the mean length. For a length distribution with a mode located in one interval, three intervals from the mode to each side were selected. Otherwise, for a mode located in more than one interval, two intervals from the mode to each side were selected. The number of sampled shrimp was usually small for the new recruits owing to gear selectivity, and for the oldest shrimp owing to low abundance. The width of the central location in these cases was defined by recognizing a breaking point at which the smallest number was observed, e.g. 20 mm in May 88 and 32 mm in August 89 for males (Table 1). If two peaks are located closely (e.g. June and July 1988 for females), a moving average over three intervals was used to define the mode. For example, the mean numbers of shrimp over 22–24, 23–25, 24–26, and 25–27 mm were 59, 62, 62, and 58, respectively, for July 1988 females; therefore the mode was defined from 23–26 mm. If two peaks from the same cohort were located far from each other (e.g. September 1988), they were consid-

Table 1

Monthly carapace length (CL) frequency of male green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters sampled by RV surveys in 1988 and 1989. The bold numbers indicate the range of the central location used to calculate the mean length.

CL (mm)	1988							1989							
	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
12	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
15	4	0	0	0	0	0	0	0	0	0	0	12	0	1	0
16	2	0	3	0	0	0	0	0	0	0	0	17	0	0	0
17	4	1	7	0	0	0	0	0	0	0	0	19	0	0	0
18	3	3	7	0	2	0	0	0	0	0	0	23	5	0	0
19	3	8	24	0	0	0	0	0	0	0	0	9	6	3	6
20	0	28	24	3	2	0	0	0	0	0	0	6	3	6	8
21	1	48	46	4	15	0	0	0	0	0	0	9	25	12	25
22	1	52	59	13	51	0	0	0	0	0	0	9	24	17	35
23	1	59	66	29	59	0	0	0	0	0	0	4	52	30	70
24	1	43	59	44	99	2	0	0	0	0	0	0	75	42	96
25	1	35	55	78	75	4	1	1	0	0	0	2	159	34	173
26	0	26	21	72	68	4	3	0	0	0	0	0	32	23	255
27	2	6	31	94	120	8	6	1	0	0	1	0	16	22	343
28	4	6	10	110	180	27	6	1	1	1	3	1	10	12	127
29	5	7	1	56	230	48	12	2	1	2	4	1	18	3	46
30	6	6	1	21	169	83	27	4	5	3	5	1	3	3	1
31	5	6	1	12	37	54	40	19	9	16	14	2	2	3	1
32	3	2	0	1	10	12	42	16	19	24	48	7	4	3	1
33	5	2	0	3	1	4	17	14	17	25	46	7	4	3	1
34	3	1	0	1	0	0	11	6	3	6	25	4	5	7	2
35	1	1	0	1	0	1	2	4	2	4	7	2	4	5	3
36	2	1	7	1	3	0	1	0	1	2	4	3	1	1	3
37	0	0	0	0	3	0	0	0	2	1	4	1	0	1	0

ered to represent different recruitments, and only the one that could be followed based on biological grounds was used in growth parameter estimation (Schnute and Fournier, 1980). Recruitment was usually first detected in May or June for the spring cohort and a minor recruitment in September or October in some years (Tables 1 and 2). The birthday of the spring cohort, based on the spawning study of Mohammed et al. (1981) was considered to be January 1. The age of the 1986 spring cohort on 18 May which was the survey date was then calculated to be 4.58 months or 0.38 yr. The ages of the cohort in the following months were calculated in the same way, and the weighted mean carapace length for the cohort at each month or age was then calculated by using the defined central range (Table 3).

### Estimation of the seasonal growth parameters

The growth parameters,  $L_{\infty}$ ,  $K$ ,  $t_0$ ,  $C$ ,  $t_s$ , were estimated for males and females of the 1986, 1987, 1988, and 1989 spring cohorts (Table 4). The hypothesis of

equality of the covariance matrices between sexes or cohorts was rejected in all cases except for the comparison of 1986 and 1987 females (Tables 5 and 6). Therefore, the differences between vectors of the growth parameters were tested by using Equation 2 for all the pairs except for the 1986 and 1987 females which were tested with Hotelling's  $T^2$ . Significant differences in growth between male and female shrimp were detected ( $P < 0.005$ ) for all four cohorts (Table 5). The differences in growth of female shrimp between cohorts were not significant except for the 1986 and 1988 cohorts ( $P < 0.05$ ). The vectors of growth parameters for male shrimp differed significantly between 1986, 1987, and 1988 cohorts, but the growth of the 1989 cohort was not found to be significantly different from the others.

## Discussion

### Accuracy of the proposed method

The bootstrap technique (Efron, 1982) was applied to examine the effects of variations in length fre-

**Table 2**

Monthly carapace length (CL) frequency of female green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters sampled by RV surveys in 1988 and 1989. The bold numbers indicate the range of the central location used to calculate the mean length.

CL (mm)	1988							1989								
	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
12	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
13	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
14	1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
15	2	2	0	0	0	0	0	0	0	0	0	10	2	0	0	0
16	2	1	3	0	0	0	0	0	0	0	0	15	0	0	0	0
17	3	2	7	0	0	0	0	0	0	0	0	11	0	0	0	0
18	4	5	17	0	0	0	0	0	0	0	0	23	0	0	0	0
19	3	6	13	0	0	0	0	0	0	0	0	15	0	0	0	0
20	2	10	7	1	0	0	0	0	0	0	0	6	1	3	11	1
21	1	20	28	1	3	0	0	0	0	0	0	2	0	6	6	1
22	0	43	46	0	7	0	0	0	0	0	0	10	3	11	18	1
23	0	53	68	3	21	0	0	0	0	0	0	6	2	20	20	1
24	1	37	65	8	16	0	0	0	0	0	0	6	1	26	46	3
25	0	51	53	31	37	0	0	0	0	0	0	2	23	28	70	17
26	0	33	69	25	44	0	0	0	1	0	0	2	5	22	47	13
27	1	22	53	37	63	1	0	0	1	0	0	0	18	23	94	16
28	1	15	51	50	42	1	1	0	0	0	0	0	39	28	131	17
29	0	8	23	41	33	3	1	0	0	0	0	0	0	23	92	29
30	0	10	24	60	67	4	3	0	1	0	0	0	8	25	107	38
31	0	4	18	52	84	10	2	0	0	0	0	0	3	17	115	83
32	0	1	12	58	75	9	6	0	0	0	0	1	0	14	107	140
33	0	1	14	34	99	14	9	1	1	1	1	0	0	10	77	128
34	1	0	0	31	81	25	7	2	1	1	2	0	0	14	50	166
35	0	2	0	29	81	36	13	4	1	0	3	0	0	4	23	110
36	1	1	0	16	63	30	9	4	1	2	1	2	1	1	18	138
37	1	1	0	10	74	42	15	4	2	3	3	1	1	1	7	82
38	2	2	4	8	40	49	24	6	2	4	3	0	0	2	2	66
39	1	1	1	3	20	31	34	3	4	3	3	0	0	5	2	20
40	1	1	0	3	19	16	36	8	4	3	3	1	0	1	2	25
41	1	3	0	2	0	21	31	10	4	10	7	1	4	1	5	16
42	3	0	0	0	3	10	29	10	6	14	9	2	3	1	17	0
43	1	0	0	1	4	0	20	7	7	15	12	2	4	1	0	0
44	4	1	1	2	0	4	13	5	4	17	16	4	3	1	1	0
45	2	3	1	1	0	2	9	3	3	15	18	5	5	2	1	0
46	2	1	1	1	0	1	5	2	3	12	11	4	3	4	0	0
47	4	2	7	1	1	1	0	1	3	7	9	4	4	2	0	0
48	2	1	7	0	0	0	1	0	0	4	5	3	2	2	2	2
49	1	0	0	1	2	0	1	0	0	1	1	1	0	1	0	0
50	1	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0
51	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0

quency on the growth estimates by the proposed method. The monthly length-frequency data in Table 1 were resampled 100 times with replacement and thus 100 length-frequency data sets were generated which were used to estimate the growth parameters with the proposed method in this study. The bias caused by the variations in length-frequency distributions was estimated from 100 bootstrap estimates compared to the true value, i.e.  $bias = estimate - true$  for  $K$ ,  $t_0$ ,  $C$ , and  $t_s$ , and  $bias = (estimate - true)/10$  for  $L_\infty$ . The boxplot (Fig. 1) showed that the bias distri-

butions were fairly symmetrical, and the medians of the biases in bootstrap estimates for growth parameters, shown as a bar in the box of the boxplot, were located very close to the center of the box and to the horizontal zero line. The means of  $L_\infty$ ,  $K$ ,  $t_0$ ,  $C$ , and  $t_s$  from 100 bootstrap estimates were 35.88 mm, 1.98  $yr^{-1}$ , -0.06 yr, 0.73, and -0.41 yr which were very close to the true values (Table 4). The bootstrap simulations indicated no trend of over- or under-estimation of the growth parameters by the proposed method. The proposed method works well for green

tiger prawns in Kuwait waters because this species is short lived and has only one main recruitment (van Zalinge, 1984) so that different cohorts can be recognized clearly and the central location of the length distribution for each cohort can be defined easily. This

method may be used for other short lived species with discontinuous recruitment.

The sensitivity of the growth estimates to the subjective selections of the spread width of the central location was investigated with the length-frequency

**Table 3**

Carapace length (CL) at age of male and female green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters for cohorts 1986–89.

Month	1986			1987			1988			1989		
	Age (yr)	CL ♂ (mm)	CL ♀ (mm)	Age (yr)	CL ♂ (mm)	CL ♀ (mm)	Age (yr)	CL ♂ (mm)	CL ♀ (mm)	Age (yr)	CL ♂ (mm)	CL ♀ (mm)
May	0.38	19.39	21.11	0.36	—	15.23	0.39	16.91	17.71	0.39	17.55	17.54
Jun	—	—	—	0.44	23.26	24.22	0.49	22.86	23.94	0.44	23.57	23.58
Jul	0.55	25.04	27.92	0.55	24.41	25.54	0.53	23.02	24.72	0.52	24.26	25.02
Aug	0.61	26.95	30.02	0.61	27.16	30.74	0.63	27.24	30.77	0.60	26.36	28.39
Sep	0.73	28.11	32.65	0.69	27.84	33.33	0.70	28.57	32.98	0.70	28.40	33.97
Oct	0.78	29.32	37.41	0.78	29.67	36.80	0.78	29.84	37.64	0.83	30.28	39.09
Nov	0.86	30.07	39.28	0.86	29.26	40.04	0.85	31.38	40.11	0.89	31.67	42.63
Dec	0.94	30.65	40.60	0.97	31.57	42.70	—	—	—	0.95	31.47	41.99
Jan	1.03	31.42	40.90	1.05	32.30	41.94	1.03	31.92	41.59	1.04	31.89	41.37
Feb	1.11	30.35	40.29	1.12	32.33	43.03	1.12	32.16	42.48	1.11	31.71	42.91
Mar	1.19	31.41	43.44	1.20	32.10	43.14	1.21	32.36	43.89	1.19	31.93	43.27
Apr	1.28	30.69	44.82	1.28	32.73	44.53	1.29	32.64	44.47	1.29	32.43	44.03
May	1.36	31.32	45.28	1.39	33.15	46.77	1.39	32.73	45.30	1.37	32.48	45.05
Jun	1.44	32.75	45.33	1.49	33.46	45.76	1.44	33.69	44.82	1.48	33.41	45.39
Jul	1.55	34.31	45.40	1.53	34.45	47.37	1.52	33.99	46.13	1.52	33.33	45.06
Aug	1.61	33.86	46.34	1.63	34.23	47.13	1.60	34.76	47.86	1.58 <sup>1</sup>	34.63	45.68
Sep	1.69	—	46.71	1.70	—	49.24	1.70	—	47.78	—	—	—

<sup>1</sup> The survey date was 28 July 1990.

**Table 4**

Growth parameters of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters estimated by using the proposed method. SE represents the standard error.  $L_{\infty}$  is the asymptotic length;  $K$  is the intrinsic growth rate;  $t_0$  is the age at which the length of the animal is 0; and  $t_s$  and  $C$  are the parameters defining the seasonal growth patterns.

Cohort	$L_{\infty}$	SE	$K$	SE	$t_0$	SE	$t_s$	SE	$C$	SE
	(mm)		(yr <sup>-1</sup> )		(yr)		(yr)			
♂	37.83	1.92	1.15	0.26	-0.39	0.13	-0.43	0.03	0.96	0.18
1986										
♀	49.71	2.53	1.75	0.48	0.04	0.11	-0.22	0.12	0.25	0.23
♂	37.51	3.02	1.26	0.57	-0.39	0.30	-0.30	0.06	0.45	0.31
1987										
♀	51.13	2.30	1.81	0.41	0.10	0.08	-0.34	0.08	0.30	0.25
♂	35.88	0.76	1.95	0.27	-0.05	0.07	-0.42	0.03	0.75	0.16
1988										
♀	51.60	1.51	1.62	0.21	0.05	0.05	-0.32	0.03	0.54	0.14
♂	34.63	1.27	2.33	0.78	-0.01	0.16	-0.48	0.10	0.49	0.36
1989										
♀	47.95	3.44	2.15	0.98	0.09	0.16	-0.25	0.09	0.55	0.36

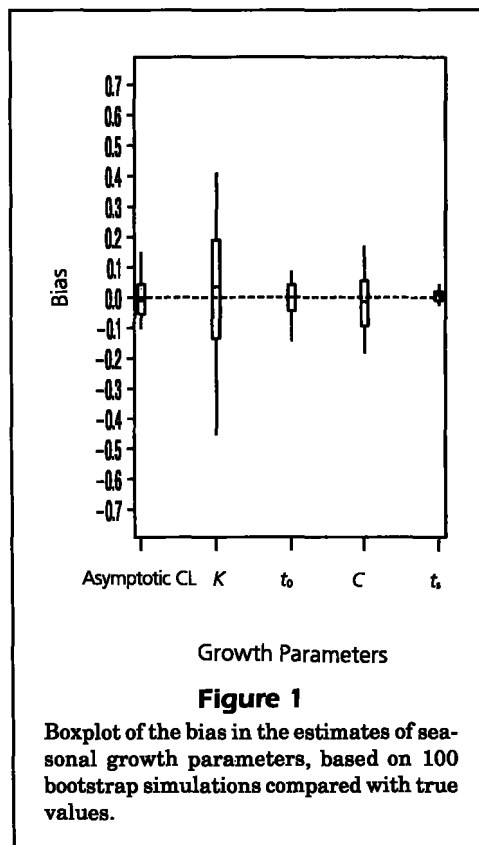
data in Table 1 by using five scenarios, i.e. modes, 1–2 mm, 2–3 mm, 3–4 mm, and as wide as possible to spread from the mode to each side. Scenario 1 is similar to the modal progression analysis (George and Banerji, 1964) and scenario 3 is the selection used in this study. The growth estimates for the five scenarios were very similar, and the growth curve estimated with scenario 3 was located in the middle of the five curves (Fig. 2). The insensitivity of the proposed method to the subjective selection of the spread width, as mentioned in the Material and Methods section, may be due to the fairly symmetri-

cal length distribution around the distinct mode of the cohort. The spread from the mode can only go up and down for 2–3 mm for the old age classes (e.g.

**Table 5**

Test of equality of covariance matrices of growth parameters between sexes using the statistic  $MC^{-1}$  and test of differences in growth between sexes of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters using the statistic  $T_v^2$ .

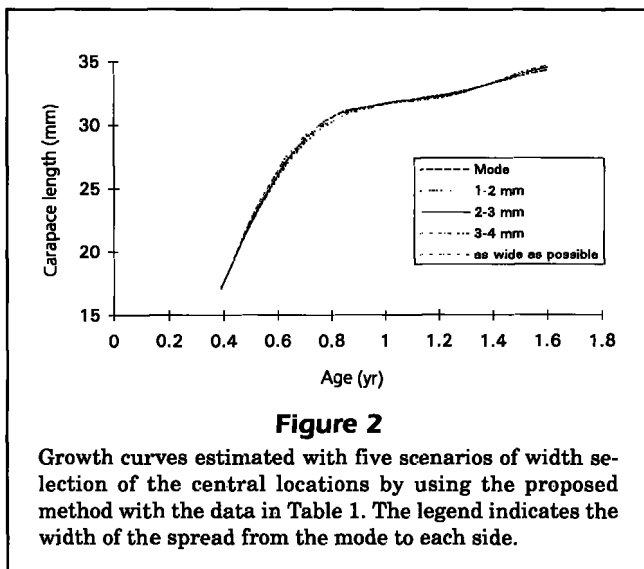
Cohorts		1986	1987	1988	1989
$H_0: \Sigma_{\delta} = \Sigma_{\varphi}$	Statistic	91.45	95.55	57.95	74.14
	v	15	15	15	15
	P<	0.005	0.005	0.005	0.005
	$\chi^2_{0.005; 15}$	32.8	32.8	32.8	32.8
	Statistic	392.53	664.87	445.76	281.05
$H_0: \beta_{\delta} = \beta_{\varphi}$	v	5	5	5	5
	P<	0.005	0.005	0.005	0.005
	$\chi^2_{0.005; 5}$	16.7	16.7	16.7	16.7



**Table 6**

Test of equality of covariance matrices of growth parameters between cohorts using the statistic  $MC^{-1}$  and test of differences in growth between cohorts of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters using Hotelling's  $T^2$  for the pair of 1986 and 1987 cohorts of female and  $T_v^2$  for the rest.

Cohorts		1987	1988	1989	
$H_0: \Sigma_i = \Sigma_j$	$\delta$	1986	47.09 ( $P < 0.005$ )	99.20 ( $P < 0.005$ )	124.79 ( $P < 0.005$ )
		1987	—	115.99 ( $P < 0.005$ )	122.66 ( $P < 0.005$ )
		1988	—	—	69.48 ( $P < 0.005$ )
	$\varphi$	1986	18.92 ( $P > 0.1$ )	47.37 ( $P < 0.005$ )	67.96 ( $P < 0.005$ )
		1987	—	46.94 ( $P < 0.005$ )	52.74 ( $P < 0.005$ )
		1988	—	—	81.85 ( $P < 0.005$ )
	$\delta$	1986	16.19 ( $P < 0.01$ )	26.73 ( $P < 0.005$ )	6.26 ( $P > 0.25$ )
		1987	—	37.49 ( $P < 0.005$ )	8.02 ( $P > 0.1$ )
		1988	—	—	6.46 ( $P > 0.25$ )
$H_0: \beta_i = \beta_j$	$\varphi$	1986	1.45 ( $P > 0.1$ )	12.30 ( $P < 0.05$ )	6.59 ( $P > 0.25$ )
		1987	—	1.50 ( $P > 0.9$ )	4.28 ( $P > 0.5$ )
		1988	—	—	4.54 ( $P > 0.25$ )



June and July 1989) in order to avoid the overlapping part with other cohorts; therefore, the ranges of the central locations for these length distributions were the same for scenarios 3, 4, and 5. This may reduce the variations in growth parameters estimated by the five scenarios and indicates that the spread of 2–3 mm is a reasonable choice.

### Comparison between the ELEFAN I, Bhattacharya, and proposed methods

Statistical tests with the modified Hotelling's  $T^2$  statistic (Hanumara and Hoenig, 1987) and Equation 2

indicated no significant difference ( $P > 0.1$ ) in growth parameters estimated by the proposed method and the Bhattacharya method (Table 7) with the same length-frequency data. The Bhattacharya method estimates the population density function of the length-frequency distribution for a cohort on the basis of the normal assumption; therefore, the method requires very complicated calculations and involves a subjective selection of the estimated population density function (Pauly and Caddy, 1985). The proposed method, however, avoids the tedious calculations. Therefore, the sophisticated computer packages for length-frequency analysis are not necessary with the proposed method. Moreover, at least for the oldest age class of green tiger prawns, to define the width of the central location is more objective than to define the population density function. The Bhattacharya method has an advantage over the proposed method in that it estimates the mean length at age with standard deviation, which can be used to estimate the degree of overlap among cohorts (McNew and Summerfelt, 1978).

It is impossible to compare the proposed method with ELEFAN I by an analytical approach because ELEFAN I cannot estimate the variances of the growth parameters. The growth parameters estimated by using ELEFAN I (Table 8) with the same length-frequency data were similar to those estimated by the proposed method, although the parameter  $K$  estimated by ELEFAN I tends to be lower (six out of eight) and the parameter  $C$  tends to be higher (six out of eight). The simulation studies by Rosenberg and Beddington (1987) and Isaac (1990)

**Table 7**

Growth parameters of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters estimated by using Bhattacharya method. SE represents the standard error.

Cohort	$L_{\infty}$	SE	$K$	SE	$t_0$	SE	$t_s$	SE	$C$	SE
	(mm)		(yr <sup>-1</sup> )		(yr)		(yr)			
1986										
♂	39.01	1.87	1.08	0.22	-0.39	0.12	-0.45	0.03	0.80	0.15
♀	48.91	1.77	1.85	0.39	0.04	0.08	-0.21	0.06	0.43	0.17
♂	36.20	2.59	1.43	0.68	-0.36	0.31	-0.27	0.06	0.57	0.34
1987										
♀	51.29	2.60	1.49	0.36	-0.07	0.11	-0.23	0.03	0.69	0.20
♂	35.42	0.62	2.16	0.27	-0.01	0.06	-0.44	0.03	0.76	0.16
1988										
♀	51.00	1.76	1.68	0.26	0.06	0.06	-0.32	0.03	0.51	0.17
♂	34.39	1.10	2.89	1.06	0.11	0.16	-0.57	0.15	0.47	0.32
1989										
♀	47.02	2.83	2.48	1.16	0.14	0.16	-0.22	0.12	0.52	0.33



**Table 8**

The growth parameters of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters estimated by using ELEFAN I. WP represents winter point.

Cohort	$L_{\infty}$ (mm)	$K$ ( $\text{yr}^{-1}$ )	WP (yr)	$C$
♂	36.13	1.5	0.50	0.7
1986				
♀	49.87	1.6	0.40	1.0
♂	36.83	1.5	0.10	0.6
1987				
♀	52.13	1.6	0.45	0.5
♂	37.13	1.6	0.10	0.8
1988				
♀	50.88	1.6	0.20	0.6
♂	36.13	1.4	0.20	0.8
1989				
♀	49.00	1.7	0.20	0.5

suggested that ELEFAN I underestimates the true value of  $K$ , and Rosenberg and Beddington (1987) concluded that ELEFAN I estimated  $K$  reliably only if the true value of  $K$  was known within about 25%. ELEFAN I also tends to have multiple maxima of the score function (Rosenberg and Beddington, 1987; Isaac, 1990), as found for the SLCA method (Basson et al., 1988; Isaac, 1990), which makes it difficult to select the best set of growth parameters from the multiple solutions. The proposed method has the advantage over ELEFAN I in that it applies a non-linear least-squares technique with the Gaussian iterative method (SAS, 1992) for solution searching, which is more sensitive in defining the best set of growth parameters and which estimates variances and covariances for the growth parameters so that the growth between cohort and sexes can be compared statistically.

Castro and Erzini (1988) studied the effect of different recruitment patterns on ELEFAN I (Pauly and David, 1980) and modal progression analysis implemented in LFSA (Sparre, 1987b) with simulated length-frequency data. The results were generally encouraging, and ELEFAN I produced better estimates than did modal progression analysis for the case of multiple recruitment per year. However, for both methods, multiple recruitment makes it difficult to estimate growth parameters (Castro and Erzini, 1988). The recruitment pattern of green tiger prawns in Kuwait waters is relatively simple and the degree of overlap between cohorts is low. It would be worthwhile to test the performance of the proposed method for species with more complicated recruit-

ment patterns and high overlapping cohorts with real or simulated data.

### Implication of the variations in growth

The highly significant differences in growth between sexes of green tiger prawns is not surprising because female shrimp grow to be much larger than males. Female and male green tiger prawns in Kuwait waters are distributed in the same area and experience the same environmental changes, but the annual variations in growth curves between cohorts are more obvious for males than for females (Table 6). These variations suggest that the responses of the female and male shrimp to environmental factors might be different, and that the growth of males may be more vulnerable to environmental changes. A possible reason that females are less sensitive to environmental change is that they have more energy reserves that can be utilized to maintain homeostasis by shifting from anabolism to catabolism (Pickering, 1981). Female shrimp grow faster and become larger than males, have lower natural mortality, but with a higher market demand suffer higher fishing mortality (Xu et al., 1995) compared with males. All these differences between female and male shrimp should be taken into consideration when monitoring the shrimp fisheries, estimating the population abundance and biomass, and formulating management policy.

### Acknowledgment

This research was part of the Shrimp Fisheries Management Project sponsored by Kuwait Institute for Scientific Research, the United Fisheries of Kuwait, and the Public Authority for Agriculture and Fisheries. The contributions of the Shrimp Fisheries Management Project staff to the continuous four-year research-vessel surveys formed the basis for this research. G. R. Morgan, J. M. Bishop, and two anonymous reviewers provided very helpful comments on the manuscript.

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