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Spatial variation in growth of the green tiger prawn (*Penaeus semisulcatus*) along the coastal waters of Kuwait, eastern Saudi Arabia, Bahrain, and Qatar

Y. Ye, J. M. Bishop, N. Fetta, E. Abdulqader,
J. Al-Mohammadi, A. H. Alsaffar, and S. Almatar

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Shrimp (*Penaeus semisulcatus*) length-frequency data collected from the coastal waters of Kuwait, Saudi Arabia, Bahrain, and Qatar during a 23-month study from 1999 to 2001 were analyzed to estimate parameters of von Bertalanffy growth equation. All growth curves show a strong seasonal oscillation and a difference in size between males and females. The estimates of l_∞ exhibit a southward decreasing trend with increasing temperature and salinity. A single variable of annual mean temperature explains 94 and 81% of the variations in l_∞ for males and females, respectively. Likelihood ratio tests compared growth parameters among survey areas. A significant difference in growth was found between Kuwait and Kufji, and between Manifa and Dareen. Based on these results, we conclude that three separate populations of *P. semisulcatus* are present in the western Arabian Gulf: one in Kuwait, one in Kufji and Manifa, Saudi Arabia, and a third occupying Dareen, Saudi Arabia, Bahrain, and Qatar waters. Countries sharing unit stocks should implement a cooperative approach to the management of each.

Keywords: growth comparison, spatial variation, shared stocks, Arabian Gulf.

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Y. Ye, J. M. Bishop, A. H. Alsaffar, and S. Almatar: Mariculture and Fisheries Department, Kuwait Institute for Scientific Research, Salmiya, Kuwait. N. Fetta: Directorate of Marine Resources, General Commission for the Protection of Marine Resources, Environment, and Wildlife, Sihat, Saudi Arabia. E. Abdulqader: Bahrain Centre for Studies and Research, Manama, Bahrain. J. Al-Mohammadi: Fisheries Development Section, Ministry of Municipalities and Agriculture, Doha, Qatar. Correspondence to Y. Ye; CSIRO Marine Research, PO Box 120, Cleveland, Queensland 4163, Australia; tel: +61 7 3826 7290; fax: +61 7 3826 7222; e-mail: yimin.ye@csiro.au.

Introduction

Growth parameters represent an integration of biological characteristics of a given fish species and physical features of the surrounding environment. The great spatial variation of oceanographic conditions often leads to the formation of localized fish stocks that are adapted to local environments and differ from other stocks in both biological and ecological characteristics. A single species that is distributed over a wide region often forms stocks that have different life history parameters and population dynamics. Growth parameters are fundamental in fish population dynamics studies as most mathematical models for stock assessment incorporate growth equations. Therefore, spatial variation in fish growth requires special attention in designing fishery management regulations and is critical to the development of bi-national management and resource-sharing strategies (Begg *et al.*, 1999a).

The shrimp fishery ranks among the most productive and valuable fishery in the Arabian Gulf. In the 40 years since the start of commercial fishing, landings have ranged from 3900 t in 1979 to 20 000 t in 1989 (Bishop *et al.*, 2001). Although several species contributed to the landings, green tiger prawn, *Penaeus semisulcatus*, is the dominant species, contributing about 60% of the total shrimp catch, on average, in Kuwait (Ye *et al.*, 1999) and 95% in Saudi Arabia (Sakurai, 1998). Accordingly, shrimp fishery management has focused primarily on *P. semisulcatus*.

Kuwait, Saudi Arabia, Bahrain, and Qatar are located in the northwestern coast of the Arabian Gulf (Figure 1). Each

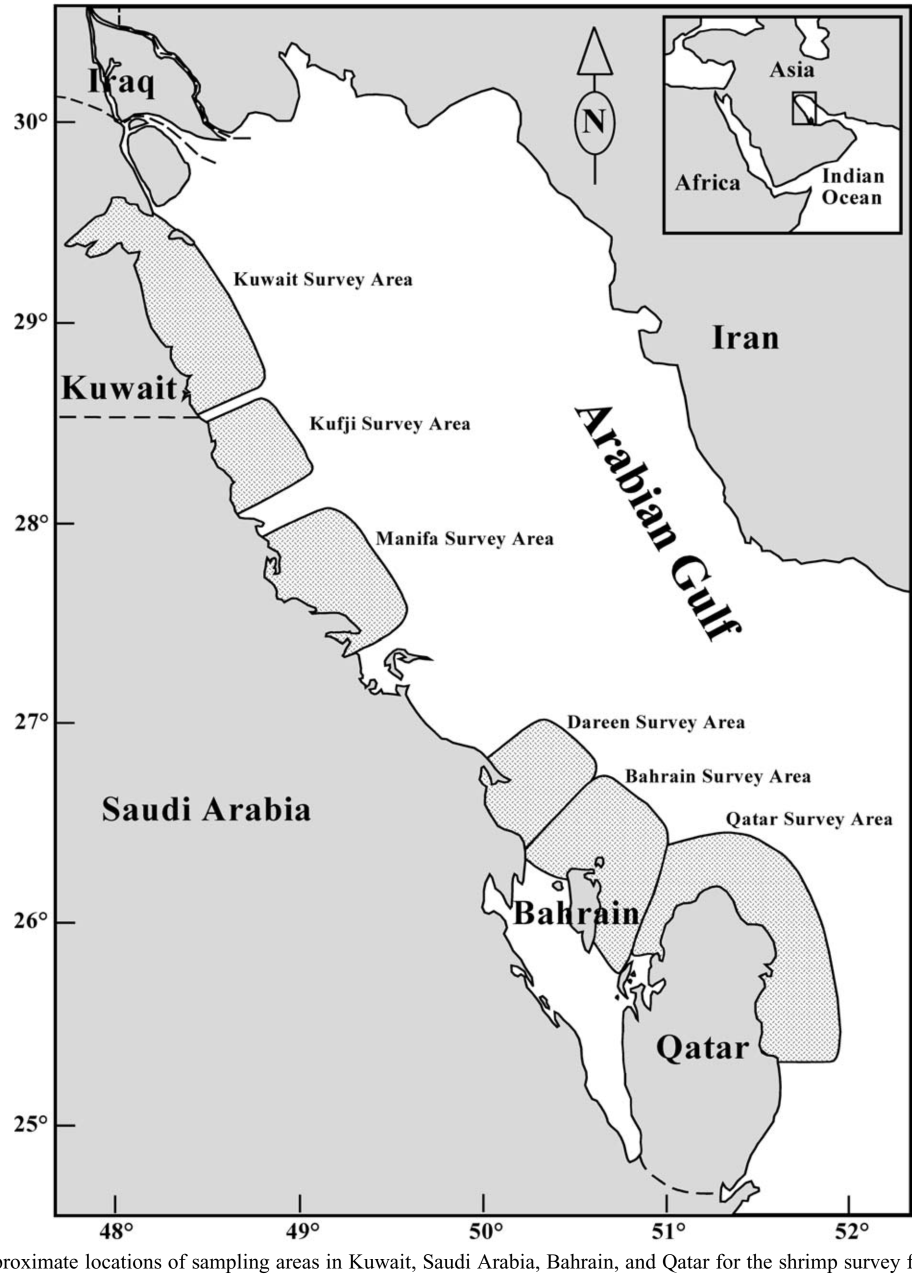

Figure 1. Approximate locations of sampling areas in Kuwait, Saudi Arabia, Bahrain, and Qatar for the shrimp survey from March 1999 through January 2001.

country exercises its sovereignty to manage shrimp fisheries within its own territorial boundaries, and the management regulations adopted by each country are different. For example, Kuwait customarily opens its fishing season on September 1 based on maximum yield per recruit analysis (Ye, 1998), but Saudi Arabia starts its season on August 1. To prevent recruitment overfishing, Kuwait closes its fishing when a spawning biomass indicator falls below a certain level (Morgan, 1989; Ye *et al.*, 1999), but there is no such reference point established in neighboring Saudi Arabia. Kuwaiti fishermen question the effectiveness of Kuwait's effort to achieve maximum yields, as they argue that their counterparts in bordering Saudi Arabia are actually depleting the Kuwaiti stock, while Kuwait's waters are closed to shrimp trawling. This has resulted in increasing pressure on management and research organizations over the last few years. Similar problems also exist between Saudi Arabia and Bahrain. If two countries share a single stock, coordinated regulation is required for effective management. Until recently, no study had addressed the issue of unit stocks between countries for their optimal management. It was believed necessary and beneficial to define management units as areas wherein shrimp have similar life history traits (Hansen and Ashcan, 2000).

This article reports the results of shrimp growth in waters of each of the four countries. By fitting the same growth curves to the data from two neighboring countries, comparison of the parameters between the two curves provides a mechanism for the comparison of populations in different areas and environments (Bernard, 1981). As only Kuwait had conducted extensive studies on life parameters and population dynamics of *P. semisulcatus*, the resulting estimates of growth parameters should also provide basic inputs to stock assessment for the other countries.

Materials and methods

The data

A 3-year shrimp survey project in coastal waters of the four countries was initiated in 1998 under the auspices of the Gulf Cooperation Council. Field sampling covered a 23-month period, beginning in March 1999 and continuing monthly through January 2001. The survey covered six areas that were known or suspected shrimping grounds in each country's coastal waters (Figure 1). Each month, an average of 95 stations was trawled with 19 stations in Kuwait, 33 stations in Saudi Arabia (nine stations in Kufji, 14 stations in Manifa, and 10 stations in Dareen), 26 stations in Bahrain, and 17 stations in Qatar. All trawl nets used in the study were of a uniform design and fabricated by a single net maker in Bahrain, although different countries used different styles of vessels to conduct the sampling. Industrial shrimp trawlers towing two nets were used in Kuwait, Kufji, and Manifa, and dhow boats towing a single net were used in Dareen, Bahrain, and Qatar. All survey cruises had scientists on board who had project-oriented training to ensure uniform sampling and data quality.

Trawl stations were selected randomly for each shrimping area, except Kuwait that has been using a more complex stratified random sampling procedure for years in its survey. Trawling operations were completed in 3 days within the initial 10 days of the month. A 30-min tow was conducted at each sampling station at an average speed of 3.3 knots. All or a 3- to 5-kg subsample of the shrimp catch was analyzed for catch composition and biological information. Sample processing consisted of separating each sample by species, weighing each species by sex, and measuring carapace lengths (CL) to the nearest millimeter. CL was defined as the distance between the posterior edge of the orbit and the dorsal posterior edge of the carapace. The monthly length-frequency data were standardized to an average by dividing each length-frequency with the number of stations sampled that month. For industrial trawlers towing two nets, the two samples obtained simultaneously at each station were first averaged in the standardization. This resulted in a monthly length-frequency distribution per station based on a single net towed 1 h at 3.3 knots (Figure 2).

P. semisulcatus is gonochoristic and has a life span of about 12–18 months (Morgan, 1995). The female lays demersal eggs in offshore waters, and the larvae and the first post-larvae are planktonic. The post-larvae migrate to inshore waters, where they assume a benthic lifestyle and grow rapidly. As subadults, they return to offshore areas before the spawning season starts (Garcia and Le Reste, 1981). The absence of skeletal parts, which can be used for age determination, makes growth studies based on length-at-age data impossible. Consequently, length-frequency data have been used for growth studies. *P. semisulcatus* exhibits a prolonged spawning period covering months, the timing of which depends on the fishing ground (Bishop *et al.*, 2001). In general, spawning tends to be more seasonal for more northerly fishing grounds, i.e. Kuwait and Kufji. Commercial shrimp catches in Kuwait consist mainly of the spring cohort (for a review on biology and fisheries of the shrimp species see Ye *et al.*, 1999). The survey was therefore designed originally to cover two spring cohorts. However, insufficient funding of the project cut short the length of some country's survey, and unforeseen problems forced other countries to cancel sea cruises in some months. Kuwait carried out the longest survey from March 1999 through to January 2001, but even this survey did not cover two spring cohorts. Consequently, only the length-frequency data covering the 1999 spring cohort, i.e. from April 1999 to August 2000, were used to estimate the seasonal growth equation.

Estimation of growth parameters from length-frequency data

Various methods have been developed to estimate growth parameters from length-frequency data. George and Banerji (1964) developed a modal-class progression analysis. Pauly and David (1980) integrated the modal-class progression analysis with Peterson's (1891) method into single computer software of Compleat ELEFAN I (Pauly, 1987; Gayanilo *et al.*, 1989), later ELEFAN II and most recently as an integrated component of FiSAT (Gayanilo and Pauly, 1997). It has been widely applied in growth studies, especially in tropical and subtropical countries. Shepherd (1987) proposed the SLCA method that performs an analysis similar to ELEFAN I in that both methods estimate 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 Bravington, 1992). Other methods for analysis of length-frequency distributions are based on the normal distribution assumption of the length frequency for each cohort (Harding, 1949; Cassie, 1954; Tanaka, 1956; MacDonald and Pitcher, 1979; Sparre, 1987; Fournier *et al.*, 1990).

All these methods depend on information on central location of the length-frequency data. The central location

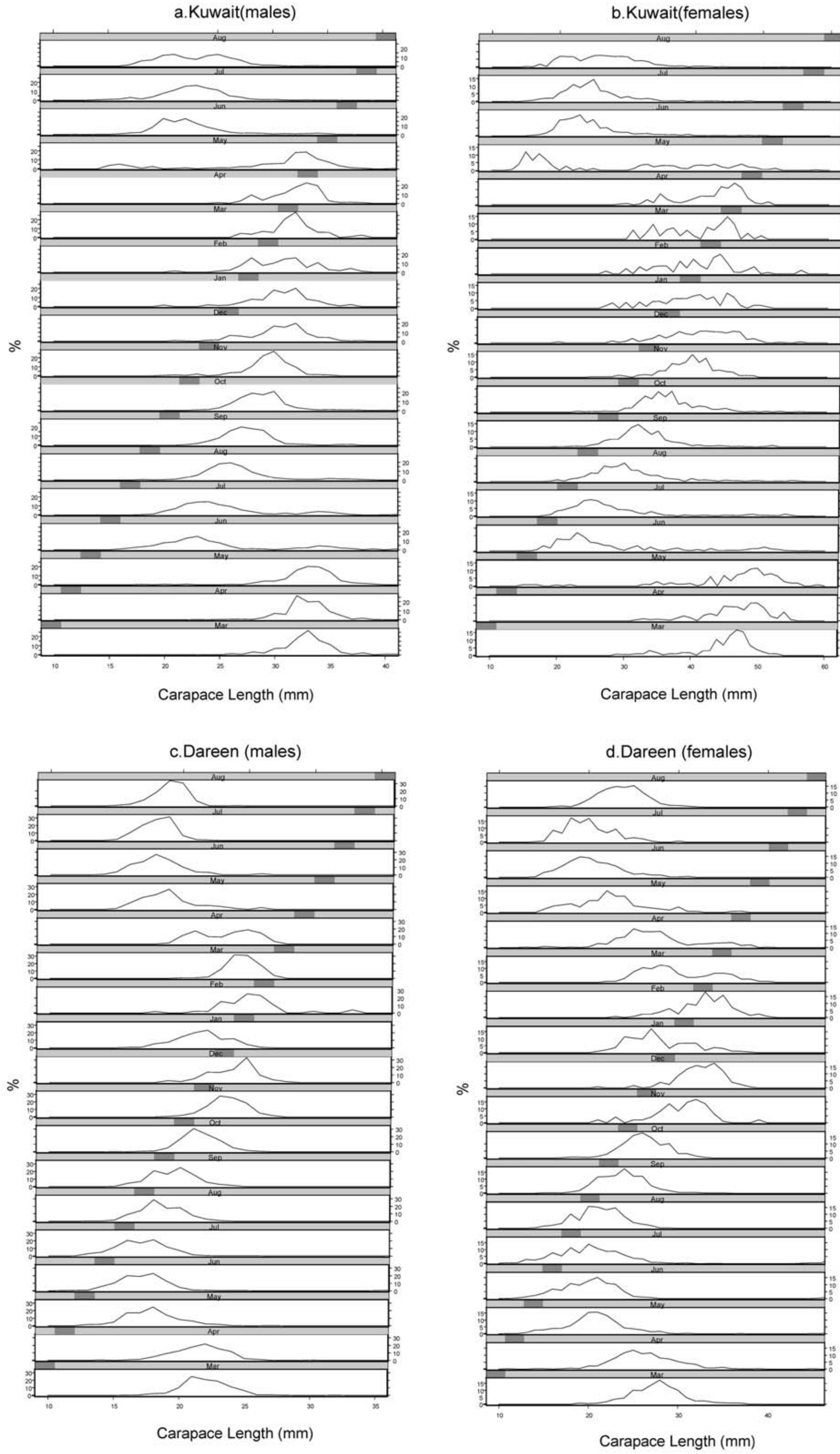

Figure 2. Monthly length-frequency distributions of *P. semisulcatus* from March 1999 through August 2000 in Kuwait [(a) males and (b) females] and Dareen waters [(c) males and (d) females].

of a distribution, however, can be many measures, such as the mode if the distribution is symmetric, the median, the mean, and the trimmed mean (Xu and Mohammed, 1996). For a species like *P. semisulcatus*, which has multiple overlapping cohorts in length distribution, it is impossible to estimate the mean, median, and trimmed mean without an assumption of the mixture of the components in the distribution. Following the ideas of trimmed mean and mode, Xu and Mohammed (1996) proposed a Central-Location Measure (CLM) to estimate growth parameters from length-frequency data. The CLM first defines a central location by the mode with a certain amount of spread. A central value can then be estimated from this spread and used to represent the mean length of the cohort at a certain time point. However, the estimated mean length from several intervals around the mode should be more robust than just using the mode representing the growth of a cohort, especially when the length distribution is skewed, which is often the case for small-size samples (Xu and Mohammed, 1996). After the estimation of mean length for all the time series of length-frequency distributions, normal non-linear fitting techniques, such as least-squares and maximum likelihood method can be applied to estimate growth parameters.

The purpose of this growth study for *P. semisulcatus* was not limited to the estimation of growth parameters. Comparison of growth differences between neighboring countries was another major concern. A multivariate comparison of growth parameters can be done by means of Hotelling's T^2-test (Kingsley, 1979; Bernard, 1981) or the likelihood ratio test (Kimura, 1980; Ceratto, 1990). ELEFAN I and II cannot estimate the variances and covariances of the growth parameters that are required for T^2-test, nor can they estimate the likelihood of the fitting. It is, therefore, impossible to make growth comparison with the parameter estimates from ELEFAN I or II. In contrast, the CLM (Xu and Mohammed, 1996) can apply either the maximum likelihood method or the non-linear least-squares technique to estimate growth parameters together with their variances and covariances, so that the growth between areas or sexes can be compared statistically. The Bhattacharya (1967) method can split a composite distribution into separate normal distributions, but requires complicated calculations and involves a subjective selection of the estimated population density function (Pauly and Caddy, 1985). The CLM avoids the tedious calculation and produces reliable results (Xu and Mohammed, 1996). Therefore, to estimate growth parameters from length frequencies, the CLM (Xu and Mohammed, 1996) was employed in this study.

Growth modelling

P. semisulcatus exhibits a strong seasonal oscillation in growth in the Arabian Gulf (Ye *et al.*, 1999). The growth model that incorporates explicit parameters defined by season and best accounts for seasonal oscillation is probably Pauly's modified von Bertalanffy growth equation (Pauly and Gaschuts, 1979)

$$l_t = l_\infty\left[1 - \exp\left(-k\left(t - t_0 + \frac{C}{2\pi}\sin 2\pi(t - t_s)\right)\right)\right] \qquad (1)$$

where l_t is the CL (mm) at time t (month), l_∞ the asymptotic length, k a curvature parameter, t_0 time when length is zero, C a constant that expresses the intensity of growth oscillation, and t_s is the summer point when shrimp grow fastest and related to the winter point (WP) by $WP = t_s + 0.5$.

The above five parameters were estimated simultaneously by fitting the length-frequency data collected during the survey from each area to the sex-specific seasonal growth equation because previous studies showed a great difference in growth between male and female. The median birthday of the spring cohort, based on the spawning study of Mohamed *et al.* (1981), was considered to be January 1, and the age of the cohort on the survey date each month was then calculated accordingly.

Comparison of growth between the survey areas

Fish growth is a complex process. To study its difference between stocks from different environments, we must use certain parameters to summarize the essential aspects of growth. One of the most common and powerful techniques used is to fit an appropriate model to data sets and then compare the resulting parameters. Given, that one has an interest in comparing the seasonal von Bertalanffy parameters (Equation (7)), there are two approaches available. One is univariate comparisons based on t- or χ^2-test statistics (Gallucci and Quinn, 1979; Kingsley, 1979; Misra, 1980, 1986). The other is to compare all the parameters of the growth equation simultaneously through multivariate Hotelling's T^2-test (Kingsley, 1979; Bernard, 1981) or likelihood ratio statistics (Kimura, 1980). The correlations among parameters in growth models make univariate statistical tests inappropriate when comparing differences between like parameters from two groups of fish (Bernard, 1981). Of the two multivariate comparisons, a likelihood ratio test was more reliable than the Hotelling's T^2-test (Ceratto, 1990) and, therefore, was employed in this study and detailed as follows.

Suppose the von Bertalanffy parameters in two samples were expressed as column vectors

$$\theta_1 = \begin{pmatrix} l_{\infty 1} \\ k_1 \\ t_{01} \\ C_1 \\ t_{s1} \end{pmatrix} \quad \text{and} \quad \theta_2 = \begin{pmatrix} l_{\infty 2} \\ k_2 \\ t_{02} \\ C_2 \\ t_{s2} \end{pmatrix} \qquad (2)$$

The null hypothesis of the likelihood ratio test comparing two growth curves is as follows (Kimura, 1980).

H_0: the parameter vectors θ_1 and θ_2 satisfy some set of q linear constraints of the form

$$\theta_{j1} = \theta_{j2} \quad j = 1 \ldots q$$

where q is the number of parameters in the equation. For two stocks with q = 5, the linear constraints are

$$l_{\infty 1} = l_{\infty 2},\ k_1 = k_2,\ t_{01} = t_{02},\ C_1 = C_2,\ \text{and}\ t_{s1} = t_{s2}.$$

This is to be tested against the alternative hypothesis (Kimura, 1980)

H_A: the parameter vectors θ_1 and θ_2 possibly satisfy no linear constraints, i.e.

$$\theta_{j1} \neq \theta_{j2} \quad j = 1 \ldots q$$

When the variances in growth estimates between stocks are not equal, the weighted sum of squares of residuals is defined as

$$S'(\theta_1, \sigma_1^2, \theta_2, \sigma_2^2) = \sum_{i=1}^{2} \sum_{t=1}^{n_i} \frac{1}{\sigma_i^2} (l_{it} - \hat{l}_{it})^2 \qquad (3)$$

where l_{it} is the tth observation from the ith sample, $\hat{l}_{it}$ is the corresponding model estimated, which is a function of parameter θ and age t, and n_i is the number of age group of the ith sample. The joint likelihood function under either hypothesis is

$$L(\theta_1, \sigma_1^2, \theta_2, \sigma_2^2) = (2\pi\sigma_1^2)^{-(n_1/2)} (2\pi\sigma_2^2)^{(-n_2/2)} \times \exp\left(-\frac{1}{2} S'(\theta_1, \sigma_1^2, \theta_2, \sigma_2^2) \right) \qquad (4)$$

The maximum likelihood estimates of σ_1^2 and σ_2^2 are obtained by taking the partial derivatives of the log of the likelihood function with respect to σ_1^2 or σ_2^2 and setting the resulting equations to zero. These estimates are

$$\hat{\sigma}_i^2 = \frac{1}{n_i} \sum_{t=1}^{n_i} (l_{it} - \hat{l}_{it})^2$$

for the ith sample. Because of the unequal variances, the maximum likelihood estimates $\hat{\sigma}_1^2$ and $\hat{\sigma}_2^2$ under either the null or alternative hypothesis are obtained by minimizing S'. In practice, this must be done using an iteratively reweighted least-squares procedure. In the case of the null hypothesis, the minimization is carried out subject to the q linear constraints.

The likelihood ratio is then given as

$$\Lambda = \frac{L_a(\hat{\theta}_{1a}, \hat{\sigma}_{1a}^2, \hat{\theta}_{2a}, \hat{\sigma}_{2a}^2)}{L_A(\hat{\theta}_{1A}, \hat{\sigma}_{1A}^2, \hat{\theta}_{2A}, \hat{\sigma}_{2A}^2)} \qquad (5)$$

where the subscripts a and A are used to distinguish the estimates obtained under the null and alternative hypothesis, respectively. Under the null hypothesis, the test statistic $-2\ln(\Lambda)$ converges asymptotically to a $\chi^2(q)$ distribution (Kendall and Stuart, 1967). The null hypothesis is rejected at the α level of significance when

$$-2\ln(\Lambda) > \chi_\alpha^2(q) \qquad (6)$$

Gallant (1975) shows that $\Lambda^{-2/n}$ converges asymptotically to a random variable whose distribution under the null hypothesis is a function of the F-distribution. The null hypothesis is rejected at the α level of significance when

$$\Lambda^{-2/n} > \left(1 + \frac{q}{f_1 + f_2} F^{\alpha}_{q, f_1+f_2} \right) \qquad (7)$$

where $f_i = n_i - q$. Of the two test procedures, Gallant's (1975) test leads to a more conservative result than the test statistic of $-2\ln(\Lambda)$ (Ceratto, 1990) and therefore was used in this study.

For reliability reasons, this study adopted the more conservative method based on Equation (7) (Ceratto, 1990) and the significant level was set at $\alpha = 0.01$. Male and female shrimp have quite different growth parameters and, therefore, were separated in the comparison of growth. As the purpose of this study was to test whether the shrimp from adjacent areas are from different stocks, comparison was carried out only between two neighboring areas, rather than any pair of the six survey areas.

Results

Growth parameters

Two phenomena in the growth of *P. semisulcatus* can be seen to be common to all the survey areas. One is a strong seasonal growth pattern (Figure 3), indicated by the value of parameter C (Table 1). The other is that females have a potential to grow larger than males (Figure 3), demonstrated by the larger values of l_∞ for females than those for males (Table 1).

The l_∞ estimates ranged from 38.32 to 51.27 mm CL for females and from 26.15 to 36.57 mm CL for males. Among the survey areas, Kuwait shrimp had the largest l_∞ (51.27 ± 2.32 mm CL) for females, and Dareen females had the smallest (38.32 ± 1.24 mm CL). Such a variation in size can also be seen for males. The largest males approached 36.57 ± 2.14 mm CL in Kuwait, and the smallest approached 26.15 ± 6.62 mm CL in Qatar (Table 1). Growth rate k varied from 1.64 to 3.68 year^{-1} for males, and 1.94 to 3.52 year^{-1} for females. There is a clear negative correlation between k and l_∞ (Table 1). The minimum estimate for parameter C was 0.22 and the maximum was 0.72, but the majority of the C estimates were around 0.5. The time when length was zero, t_0 varied from -0.15 to 0.29 years and t_s had a range from -0.3 to 0.07 years (Table 1).

Comparison of growth between survey areas

While estimating growth parameters and their standard errors (Table 1), the likelihood estimate for each fit was also recorded (Table 2). The null hypothesis that two populations of *P. semisulcatus* in neighboring areas have the same growth parameters was tested with the likelihood

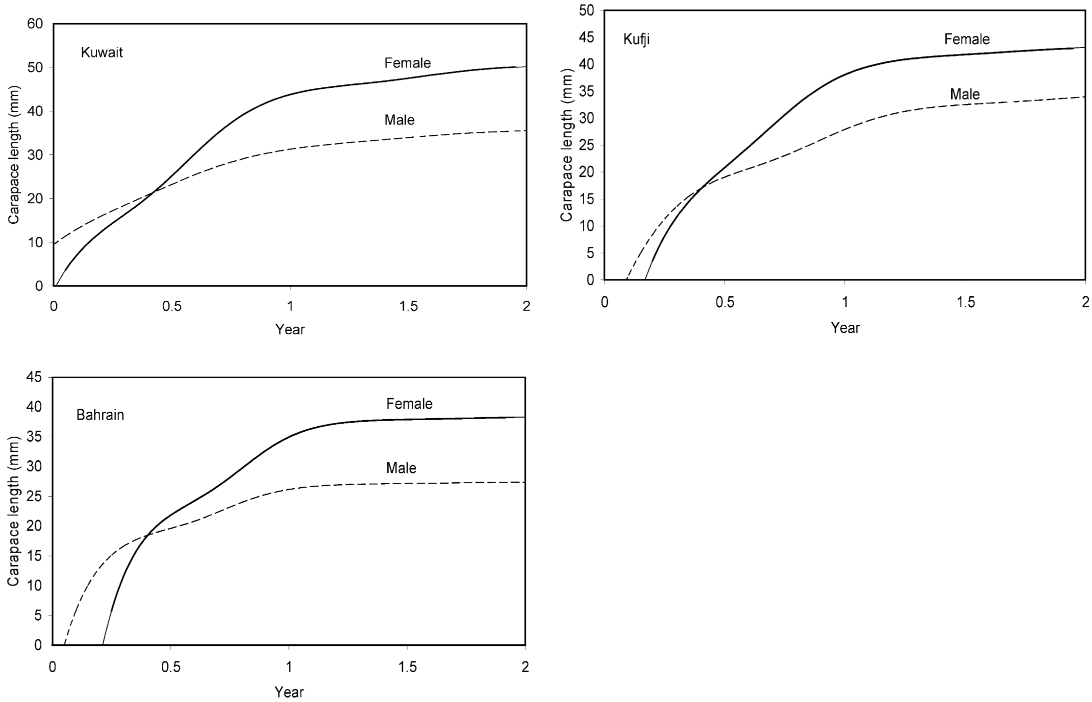

Figure 3. The estimated growth curves of *P. semisulcatus* of the 1999 spring cohort in Kuwait, Kufji, and Bahrain, representing three different stocks.

ratio method. The results show that the growth curves of both male and female *P. semisulcatus* of Kuwait's population were significantly different from those of Kufji's (Table 2). The same conclusion was also reached between Manifa and Dareen. However, no significant difference in growth of either male or female *P. semisulcatus* was detected between Dareen and Bahrain. The test results show mixed conclusions for males and females between Kufji and Manifa, between Dareen and Bahrain, and between Bahrain and Qatar (Table 2).

Discussion

Growth parameters

Among the four participating countries, only Kuwait had carried out comprehensive growth studies in the past. The results presented here are the initial estimates of growth parameters for *P. semisulcatus* based on scientific survey data in the waters off the other countries, and should be viewed as preliminary because the length-frequency data used in the analyses cover only one cohort.

Table 1. Growth parameter estimates of *P. semisulcatus* of the 1999 spring cohort for each survey area along the western coast of the Arabian Gulf with standard errors in parentheses.

Survey area	Sex	l_∞ (mm)	k (year^{-1})	t_0 (year)	C	t_s (year)
Kuwait	Male	36.57 (2.14)	1.64 (0.58)	−0.15 (0.18)	0.22 (0.28)	−0.3 (0.13)
	Female	51.27 (2.32)	1.94 (0.46)	0.08 (0.08)	0.45 (0.17)	−0.25 (0.06)
Kufji	Male	35.11 (2.58)	1.82 (0.69)	0.10 (0.14)	0.44 (0.15)	0.07 (0.05)
	Female	43.4 (8.05)	2.64 (3.52)	0.23 (0.39)	0.39 (0.29)	−0.06 (0.40)
Manifa	Male	32.66 (0.58)	3.63 (0.92)	0.25 (0.08)	0.58 (0.10)	0.03 (0.05)
	Female	43.47 (5.73)	2.34 (1.85)	0.18 (0.24)	0.3 (0.16)	−0.08 (0.29)
Dareen	Male	27.8 (9.02)	2.53 (8.89)	−0.05 (1.55)	0.72 (1.58)	−0.24 (0.58)
	Female	38.32 (1.24)	3.27 (1.23)	0.19 (0.12)	0.61 (0.12)	−0.07 (0.07)
Bahrain	Male	27.42 (0.62)	3.33 (1.39)	0.10 (0.19)	0.59 (0.09)	−0.04 (0.09)
	Female	38.37 (0.99)	3.53 (1.07)	0.29 (0.09)	0.57 (0.14)	0.05 (0.05)
Qatar	Male	26.15 (6.62)	2.09 (4.39)	−0.06 (1.04)	0.49 (0.51)	−0.02 (0.36)
	Female	38.75 (1.63)	3.23 (1.31)	0.27 (0.12)	0.51 (0.15)	−0.01 (0.09)

Table 2. The likelihood ratio tests of the seasonal von Bertalanffy growth parameters of the 1999 spring cohort *P. semisulcatus* between neighboring survey areas along the western coast of the Arabian Gulf.

Area	$L(\theta,\sigma^2)$	L_A	L_a	$\Lambda^{-2/n}$	$1+(q/(f_1+f_2))F^{\alpha}_{q,f_1+f_2}$	Test outcomes
Males						
Kuwait	−14.36	−12.74	−52.72	37.88	3.108	*
Kufji	1.62					
Kufji	1.62	0.61	−27.77	13.20	3.108	*
Manifa	−1.01					
Manifa	−1.01	−1.79	−44.12	46.91	3.108	*
Dareen	−0.78					
Dareen	−0.78	4.07	−7.56	2.89	3.108	ns
Bahrain	4.85					
Bahrain	4.85	−3.77	−36.32	19.28	3.108	*
Qatar	−8.62					
Females						
Kuwait	−16.99	−31.63	−62.50	16.41	3.108	*
Kufji	−14.73					
Kufji	−14.73	−27.59	−30.34	1.28	3.108	ns
Manifa	−12.86					
Manifa	−12.86	−23.93	−37.37	3.39	3.108	*
Dareen	−11.07					
Dareen	−11.07	−18.44	−26.74	2.13	3.108	ns
Bahrain	−7.37					
Bahrain	−7.37	−17.29	−25.15	2.04	3.108	ns
Qatar	−9.92					

*Significant at $\alpha = 0.01$; ns, non-significant at $\alpha = 0.01$.

The growth parameter estimates of Kuwait's *P. semisulcatus* (Table 1) are well in the range of previous estimates derived on the same species (Mathews *et al.*, 1987; Siddeek *et al.*, 1989; Mohammed *et al.*, 1994; Xu and Mohammed, 1996). The maximum estimate of female l_∞ was 58.00 mm CL (Mohammed *et al.*, 1996), and the minimum was 47.02 mm CL (Xu and Mohammed, 1996). Our estimate for the 1999/2000 cohort was 51.27 (±2.32) mm CL (Table 1). The estimate of l_∞ for male *P. semisulcatus* in Kuwait's waters was 36.57 (±2.14) mm CL, which also falls within the range of historical estimates from 34.39 mm CL (Xu and Mohammed, 1996) to 41.1 mm CL (Mohammed *et al.*, 1996). Estimates of other parameters, k, t_0, C, and t_s, are also comparable with those derived for various shrimp cohorts by different authors (Mathews *et al.*, 1987; Siddeek *et al.*, 1989; Mohammed *et al.*, 1994; Xu and Mohammed, 1996).

The differences in growth parameter estimates can be attributed to the following reasons. The first is the variation in shrimp growth caused by varying oceanographic conditions. With a favorable environment, a better growth is more likely, resulting in a larger body size. Because the marine environment is highly variable from year to year, inter-annual variation in growth parameters should be expected accordingly. The second is the different methods used in estimating the parameters. Each method has its strength and weakness. Even with the same set of data, the resulting estimates are likely to differ in one way or another. The third is that it is rather difficult to obtain representative size-frequency samples for all ages of the target species. A well-designed survey is the first step towards obtaining reliable estimates for growth parameters. Biased sampling can create apparent size modes or mask real ones that may be present (Hilborn and Walters, 1992), and consequently result in biased estimates. Finally, personal experiences with the fishery and in applying the length-based method are also factors in assuring the reliability of growth parameters.

Mathews *et al.* (1993) estimated l_∞ of the 1989/1990 cohort in Dareen at 55 mm CL for females and at 52 mm CL for males, with a difference of only 3 mm between sexes, which is in sharp contrast to the difference of 15–27 mm reported in Kuwait (Mathews *et al.*, 1987; Siddeek *et al.*, 1989; Xu and Mohammed, 1996) and 14.1 mm reported in Australia (Wang and Die, 1996). Mathews *et al.*'s (1993) estimates are higher than our estimates, 38.32 mm CL for females and 27.8 mm CL for males (Table 1). This discrepancy may be attributed to the sources of length-frequency data used in these two estimations. Mathews *et al.* (1993) used "a significant volume of data on length frequencies of the artisanal landings" and "from surveys, carried out on industrial vessels, usually from areas characterized by large prawns." Commercial landings usually have larger individuals than those captured by scientific surveys, and, consequently, the estimate for l_∞ is likely biased upward.

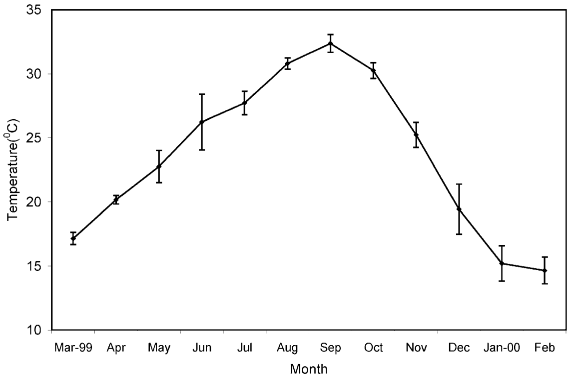

Figure 4. Seasonal pattern (±1 standard deviation) of the bottom temperature in Kuwait waters from March 1999 through February 2000.

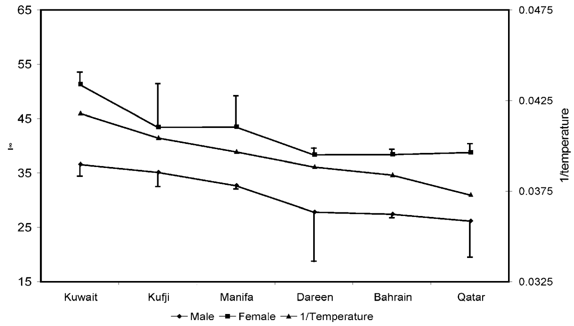

Figure 5. Comparison between the southward decreasing trend in l_∞ (±1 standard deviation) and that of the inverse of temperature during the period from March 1999 to February 2000.

The seasonal growth pattern, indicated by the value of parameter C, of *P. semisulcatus* is probably derived from the seasonal variation of the marine environment and food availability in this region. However, it is difficult to identify and measure key parameters that are directly related to the seasonal growth. Given the data available to this study, temperature may serve as a proxy parameter. A similar seasonal pattern exists in bottom temperatures in all the six survey areas. The temperature increases from March to September and then declines to a winter low in January–February with a seasonal difference in Kuwait waters of 17.7°C (Figure 4). Other shrimping grounds except Qatar showed greater differences between summer maxima and winter minima: Kufji, 22.3°C; Manifa, 22.8°C; Dareen, 21.5°C; Bahrain, 21.7°C; and Qatar, 17.7°C. It is believed that growth slows with colder temperatures and poor food availability in winter (Figure 3).

Spatial variation in shrimp growth and oceanographic variables

The growth parameters in Table 1 were derived for the same cohort using the same method, which should ensure good comparability among different survey areas. The estimates of asymptotic length for female *P. semisulcatus* show that l_∞ has the largest value in Kuwait's waters and decreases towards the south (Figure 5). A similar southward decreasing trend can also be found for estimates of l_∞ for male *P. semisulcatus* (Figure 5). Although the estimates for Dareen and Qatar have the largest standard errors, the decreasing trend appears stable and consistent with the decrease in latitude of the survey area.

Asymptotic length and growth rates are commonly inversely related. The fishing grounds in this study that produced the largest *P. semisulcatus* also showed the slowest growth rates, k (Table 1). *P. semisulcatus* from Bahrain, Dareen, and Qatar reached their ultimate size more rapidly than did those from Kuwait and Kufji. This may be partially explained because high temperatures lead to faster growth in earlier life stages of shrimp, and partially because l_∞ and k are negatively correlated in the estimation as is always the case in grow parameter estimation. The seasonal von Bertalanffy growth equation reflects several important aspects of environmental variation. For example, t_0 is related to spawning season of the species concerned, C reflects seasonal fluctuation of growth, which is most likely caused by seasonal variation in temperature and food supply, and t_s provides a time schedule when growth slows down. Oceanographic conditions are highly variable, and consequently spawning, growth and recruitment vary within a certain range. Assuming that the growth parameters are estimated precisely and reliably, then both the yearly variation in spawning season and the seasonal oscillation of shrimp growth caused by environmental changes should be reflected in the growth equation.

The spatial variation of these values probably results from differences in oceanographic conditions, with temperature and salinity being the most obvious. Average water temperature in each survey area decreased with increasing latitude from 27.9°C in Bahrain to 24.2°C in Kuwait. A simple regression of l_∞ against temperature explains 94 and 81% of the variation for males and females, respectively. Bottom salinity in the study area also showed a trend

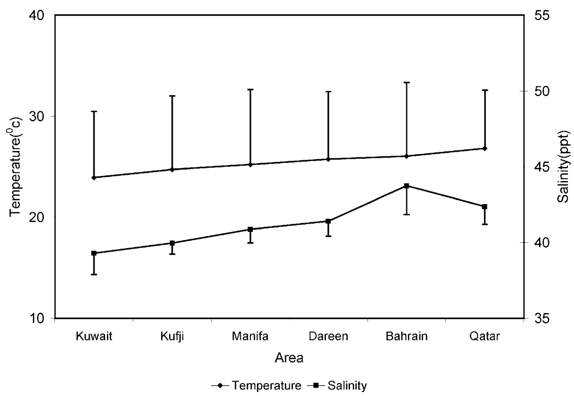

Figure 6. Average annual bottom temperatures and salinities in 1999 in the six survey areas, with standard errors shown by bars.

similar to that for temperature, averaging 44.1 psu in Bahrain and 39.0 psu in Kuwait (Figure 6). This supports the suggestion that a geographic trend of marine environments exists in the western Gulf.

Other factors, such as food availability and population density, are also important, and the interaction of all these variables would come into play for observed sizes and growth rates. For the Arabian Gulf, the Shatt Al-Arab watershed and former associated marshes in Iraq are the main sources of nutrients responsible for the northwestern Gulf productivity (Bishop *et al.*, 2001). Larger body size should be more likely in the northern nutrient-rich waters with less physiological stress when compared with southern areas like Qatar and Bahrain where the influence of nutrient supply from the Shatt Al-Arab is greatly reduced or even absent and threshold tolerance limits may occur.

Growth difference and stock identification

Growth parameters are vital for stock identification, and in turn, for effective fisheries management (Begg *et al.*, 1999a). A fish stock can be considered to be a group of different life history modes to which fish stocks have evolved. Based on this definition, a stock may exhibit differences in one or more life history parameters compared with other stocks of the same species. Given the relative ease of assessing life history parameters, differences in growth-related parameters have long been used as a basis for the identification of stocks (Begg *et al.*, 1999b).

The four participating countries border each other, and their fishing grounds are adjacent (Figure 1). Fishery management can be effective only when it is based on a single stock. If different countries share a fish stock, coordinated regulations are the only way for successful management. However, regulatory measures for shrimp fisheries in the participating countries are neither consistent nor fully supported by scientific evidence. The difficulties in establishing effective management for shrimp fisheries in these four countries are deeply rooted in the lack of knowledge about stock structure and problems in defining suitable management units. To help address this issue, this study analyzed the differences in shrimp growth among different areas. Although differences in growth parameters alone are not sufficient for stock identification, they should provide reasonable evidence as the seasonal von Bertalanffy equation incorporates several parameters reflecting environmental conditions.

Although the likelihood ratio tests for male and female *P. semisultcatus* do not lead to the same conclusion (Table 2), a more conservative inference may be reached that a significant difference in the growth of *P. semisulcatus* exists between Kuwait and Kufji, and between Manifa and Dareen. With these comparisons of growth differences, we conclude that there are three stocks of *P. semisulcatus* along the western coast of the Arabian Gulf: one in Kuwait waters, one in the coastal waters from Kufji to Manifa, and a third in the waters off Dareen, Bahrain, and Qatar.

No study has been carried out on the inter-area migration of *P. semisulcatus* in the Arabian Gulf area. Farmer and Al-Attar (1981) conducted a migratory study on *P. semisulcatus* within Kuwait's waters using tagging experiment. Local migration was found, although not conclusive due to the small number of recaptures. Abdulqader and Naylor (1995) elucidated the pattern of movement of *P. semisulcatus* in Bahrain waters on the basis of a trawling survey involving 28 stations and suggested that the north coast (of Bahrain) nursery area probably receives post-larvae from Saudi Arabia spawning grounds. Their findings are consistent with our preliminary conclusion that there is no significant difference in growth between shrimp from Dareen and Bahrain.

The tentative division of *P. semisulcatus* into three stocks in the northwest coast of the Arabian Gulf may find support from geography and oceanographic conditions (Figure 1). Kuwait is situated in the northwestern part, and, consequently, the Shatt Al-Arab discharge affects Kuwait's waters more than any of the other three countries. The effects of this influence include lower salinity, rich nutrients, and high turbidity. Higher turbidity reduces water transparency and makes shrimp less nocturnal in Kuwait than they are on shrimping grounds further south, as evidenced by the fact that Kuwait's shrimping boats operate day and night, but in other survey areas, fishermen catch shrimp only during nighttime. So, there appears to be a demonstration that Kuwait has a unique stock different from all others.

It should be remembered, however, that the three stocks of *P. semisulcatus* in the western Gulf are tentatively identified using growth parameters only. Further, the analyses were based on just one cohort. Vital population parameters for stock identification include survival, recruitment, reproduction, and abundance (Begg *et al.*, 1999b). When more parameters become available, discriminant analysis (Borges, 1995) or multivariate analysis (Kristensen, 1982) should be carried out for more conclusive results. The marine ecosystem is a very complicated integration of many variables, and oceanographic conditions for *P. semisulcatus* are expected to vary not only spatially, but also temporally. As a consequence, shrimp growth would not remain same from year to year. Temporal patterns of shrimp growth in each survey were not studied because of data limitations and require further investigation.

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