J. Mar. Biol. Ass. U.K. (2004), **84**, 351–357
Printed in the United Kingdom

Biology of the cocktail shrimp, *Trachysalambria curvirostris* (Decapoda: Penaeidae) in the Yellow Sea of Korea

H.K. Cha*, C.W. Oh† and J.H. Choi‡

*Fisheries Resources Research and Management Division, National Fisheries Research and Development Institute, Busan 619-902, South Korea. †Department of Marine Resources, Mokpo National University, Chonnam 534-729, South Korea.
‡Korea Inter-University Institute of Ocean Sciences, Pukyong National University, Busan 608-737, South Korea.
†Corresponding author, e-mail: chuloh@mokpo.ac.kr

Trachysalambria curvirostris occurs widely along the south and west coasts of Korea with a range extending from Kanghwado in the north-west, down to Sarangdo in the south-east. With seasonal warming of the waters starting in April, the shrimps begin to migrate from deep waters to the coastal area. Zoea and mysis larvae occurred from June to August. Sex ratio showed seasonal variations, with a mean value of 56.7% for the females. The species produces one cohort a year, with the ovaries ripening from June to July. Insemination appeared to take place from June to August, as more than half of the females sampled in the study over 15–16 mm carapace length were inseminated. Mean gonadosomatic index (GSI) reached a maximum between June and July. The smallest mature female found was 15 mm carapace length (CL). Size at 50% sexual maturity (CL_{50}), determined from both mature females and inseminated females, was 15.37 mm and 16.49 mm CL, respectively. Fecundity was directly proportional to the size of the female, with clutch sizes varying from 16,380 eggs in the smallest female to 114,621 eggs in the largest, and the eggs ranged from 230 μm to 340 μm in diameter. The life span of females appeared to be 14–15 months according to size frequency distributions, while that of the male was 13–14 months. Population growth was estimated by the modified von Bertalanffy growth function incorporating seasonal variation in growth. Based on the growth parameters (K=2.00 y^{-1} and L_∞=24.64 mm CL for females, and K=2.00 y^{-1} and L_∞=19.00 mm CL for males) growth curves showed that females grew faster and reached a larger size at age than males. This result is supported by differences in growth performance indices (ϕ').

INTRODUCTION

The cocktail shrimp, *Trachysalambria curvirostris* (Stimpson, 1860) (formerly known as *Trachypenaeus curvirostris*), occurs widely in coastal waters with a range extending from Korea, Japan and China westward to Malaysia, Australia, Sri Lanka, India and up to East Africa (Kim, 1977; Holthuis, 1980). Only one species of *Trachysalambria* is known to occur in coastal waters of Korea (Kim, 1977). The western coast of Korea has relatively shallow waters, with a maximum depth of only 30 m. Its waters and surrounding estuaries contain habitats important to a number of commercially important penaeid shrimps (Cha et al., 2002).

The common penaeid shrimps in the western Korean coastal waters are *Penaeus chinensis* (Osbeck, 1765), *Trachysalambria curvirostris*, *Metapenaeus joyneri* (Miers, 1880), and *Metapenaeopsis dalei* (Rathbun, 1902). *Trachysalambria curvirostris* usually inhabits the silty bottom of coastal waters in summer and moves towards deep water as the cold season advances. The depth in which the species lives and spawns ranges from 5 to 30 m in Korean waters (Kim et al., 1984).

Trachysalambria curvirostris and *Metapenaus joyneri* are target species of the stow nets and trawl fisheries from April to October in Korean waters. The major fishing area for these shrimps is centred around Oeyondo on the west coast. *Trachysalambria curvirostris* is the dominant species, contributing more than 50% of the total shrimp catch in Korea. Nevertheless, the biology of this species is poorly known. The present study is mainly focused on the distribution, migration, population properties and reproductive biology of *T. curvirostris*.

MATERIALS AND METHODS

Two sets of samples were taken: (1) monthly samples from March 1994 to December 1995; and (2) daily samples at six locations from April to December 1995 with commercial stow nets (mesh size: 0.95×0.95 mm) in waters around Oeyondo, the main fishing ground (36°15′N 126°05′E). In addition, specimens were collected along the entire coastal area of Korea from 1990 to 1996 to determine its distributional range. The samples were preserved immediately in neutralized formaldehyde. Basic hydrographic data on water temperature and salinity were collected during each sampling or plankton survey.

Plankton samples were collected from five sites on the main fishing ground. A conventional zooplankton net (330-μm mesh, 0.8 m mouth diameter) was used with a flow meter attached. Samples were preserved immediately with 5% neutralized formaldehyde. Sorting was carried out under a dissecting microscope (Wild M5). The zoeal and mysis stages of *Trachysalambria curvirostris* were distinguished using a reference collection and taxonomic criteria (Ronquillo & Saisho, 1995).

Specimens were identified to species, sexed, and measured. Total length (TL, to nearest 0.1 mm) measured from the tip of the rostrum to the end of the telson; carapace length (CL, to nearest 0.1 mm), from the posterior margin of the orbit to the posterior margin of the carapace; total weight and gonad weight (TW, GW, to nearest 0.01 g) as wet weight.

The maturity of the ovary was determined visually and the degree of maturity was divided into the following three categories after Gab-Alla et al. (1990): (1) undeveloped: ovary transparent, oocytes <0.1 mm in diameter; (2) developing: ovary cream or pale green, oocytes generally 0.1 to 0.25 mm in diameter; (3) ripe or almost ripe: ovary at full size and dark green, oocytes generally >0.25 mm in diameter. Mean egg diameter for each female was based on measurements of 200 randomly selected oocytes measured to the nearest 5 μm. Ripe ovaries were weighed, and the oocytes in a unit weight were counted to calculate fecundity. The contents of the thelycum were examined microscopically for the presence of spermatophores to determine whether or not females had mated.

Size at sexual maturity was determined separately by either the proportion of maturing and matured ovary females, or the proportion of inseminated females. The proportion of mature females by size was fitted to the logistic equation:

$$P = 1/(1 + \exp(a + b\ \mathrm{CL})) \quad (1)$$

where P is the predicted mature proportion, a and b the estimated coefficients of the logistic equation, and CL the carapace length. Parameters were estimated by nonlinear regression analysis using SYSTAT Ver. 10.0. Size at sexual maturity (CL_{50}), corresponding to a proportion of 0.5 sexually mature, was estimated as the negative ratio of the two coefficients [$CL_{50}=(a/b)$]. Any differences in the distribution of mature proportions between the two different methods were determined by the Kolmogorov–Smirnov two-sample test (Sokal & Rohlf, 1995) using SYSTAT Ver. 10.0.

Length–frequency distributions are constructed using 2 mm intervals of CL. Growth was described using the modified von Bertalanffy growth function (VBGF) (Pauly & Gaschütz, 1979):

$$L_t = L_\infty[1-\exp(-K(t-t_0)-(CK/2\pi)\sin(2\pi(t-ts)))] \quad (2)$$

where L_t is the asymptotic length, K the intrinsic growth rate, t_0 is the age at which the length of animals is 0, C the amplitude of seasonal growth oscillation, ts the age at the beginning of growth oscillation, and WP ($= ts+0.5$) the time of year when growth is slowest. Growth curves were estimated using mean carapace length and relative age. The arithmetic mean carapace length was calculated for each cohort and the normal distribution curve plotted on the length–frequency distribution. The relative ages of the modal groups are estimated as years after a birth time (based on spawning peak). At a birth time (t=0) the mean carapace length of the first zoea collected from the study area was used. A nonlinear regression model to fit the modified VBGF was used to estimate the parameters. Parameters were estimated by nonlinear regression analysis using SYSTAT Ver. 10.0. The estimates of L_∞ and K were used for composition of growth performance indices (ϕ') (Pauly & Munro, 1984) between sexes using the equation:

$$\phi' = \log_{10} K + 2\log_{10} L_\infty \quad (3)$$

RESULTS

Distribution and migration

Water temperature during the study period fluctuated seasonally in the surface layer from 6.5°C to 27.0°C and in the bottom layer from 6.9°C to 25.8°C. Salinity showed no regular seasonal pattern, ranging from 32.06 psu to 33.96 psu.

In Korea, *Trachysalambria curvirostris* occurs along the coastal area between Kanghwado on the western coast and Sarangdo on the southern coast. Fishing starts in April in the western parts of Oeyondo. With seasonal warming of the waters the shrimp migrate from deep waters to the coastal areas of the Poryoung area. From May to November the shrimps inhabit these coastal waters in water temperatures ranging from 11.6°C to 27.0°C. From early December the new generation migrates to the offshore waters, and no fishing occurs from December to March.

Larvae were collected in monthly plankton samples from April to December 1995. Zoea and mysis larvae occurred from June to August. Average density of larvae collected from five sites of the sampling area was 69 ind per 100 m^3 in June, 78 ind per 100 m^3 in July, and 39 ind per 100 m^3 in August. Larval size increased steadily with larval stages (Table 1).

Sex ratio

All specimens of *T. curvirostris* sampled from April 1994 to November 1995 were sexed during each month (Figure 1). Of the 4518 specimens, 56.7% were identified as females and 43.3% as males. A χ^2-test revealed that the number of females were significantly greater than that of males (χ^2=287.967, df=17, $P<0.001$). Males were much more abundant than females in April as the shrimp began to migrate from deep waters to the coastal waters. However from July to October the sex ratio showed a preponderance of females. These variations are not of any real biological importance. Females reach a larger size than males, and may be selectively fished by fishing gear.

Table 1. *Minimum, maximum and mean carapace length (mm) of* Trachysalambria curvirostris *larvae collected from the sampling area.*

Larval stage		Minimum	Maximum	N	Mean ±SD
Zoea	I	0.32	0.38	47	0.36 ±0.042
	II	0.46	0.52	35	0.49 ±0.052
	III	0.64	0.98	37	0.68 ±0.049
Mysis	I	0.90	1.06	31	0.93 ±0.057
	II	1.00	1.06	25	1.04 ±0.042
	III	1.12	1.24	23	1.17 ±0.085

N, number; SD, standard deviation.

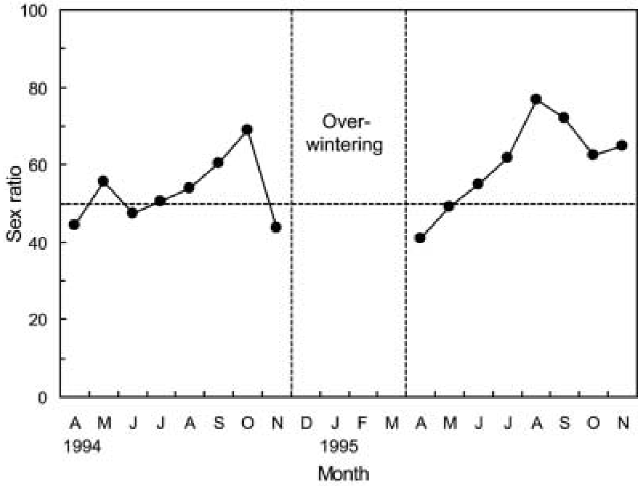

Figure 1. *Trachysalambria curvirostris*: monthly variation in the sex ratio. The horizontal dotted line indicates a ratio of 1:1 (female:male).

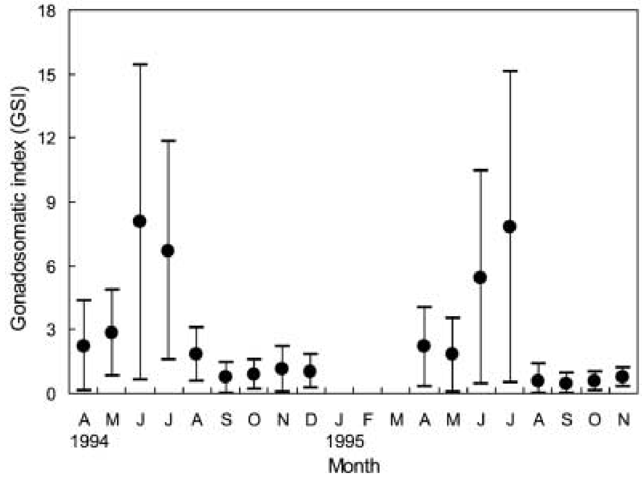

Figure 3. *Trachysalambria curvirostris*: changes in the gonadosomatic indices (GSI) in monthly samples of females during April 1994–November 1995. Solid circles indicate mean GSI, and vertical bars standard deviation of GSI.

Therefore, this ratio may not reflect true proportions in the natural population. The only firm conclusion is that for *T. curvirostris*, females represent 56.7% of the commercial catch.

Gonad maturation

The gonads were divided into three categories of development based on colour and general appearance. For each female examined, the mean diameter of oocytes, and the gonadosomatic index (GSI, ovary weight/total weight×100) were calculated. With increasing maturity the ovary became larger and GSI increased. The diameter of the oocytes varied according to developmental stage; 20–100 μm in the immature stage, 150–250 μm in the maturing stages, 230–340 μm in the mature stage (Figure 2). The mean diameter of oocytes increased with progressing the ovarian development stage with months. Mean GSI began to increase in May, and reached a maximum between June and July. It began to decrease from August (Figure 3).

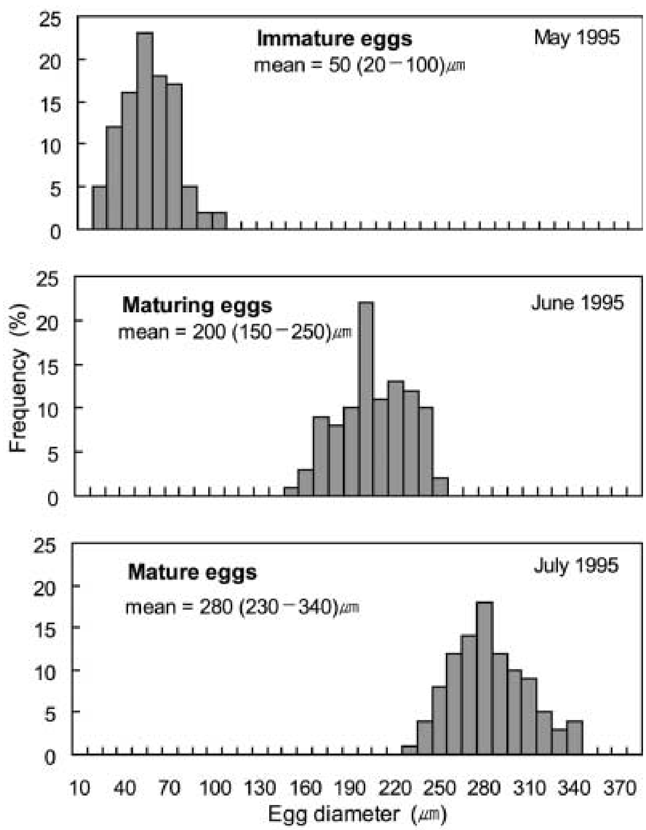

Figure 2. *Trachysalambria curvirostris*: size–frequency distribution in egg diameter.

The seasonality of breeding was investigated by examining ovary maturation, and also by determining the occurrence of inseminated females. Over 95% of ovaries were in maturing or mature stages in June and July. Insemination took place from June to August, with a peak from June to July (percentage inseminated >50%). These two results suggest that the breeding season is limited to the period June to August, with a peak from June to July.

The size at sexual maturity in females was examined using two different categories: (1) by the proportion of specimens at each size-class with maturing or mature ovaries; and (2) by the proportions of these size-classes which had been inseminated. Only females collected during the breeding season was used for this analysis. In both categories the minimum size of mature females was 15 mm CL. At larger sizes the proportion mature rose rapidly, to over 50% at 16 mm CL. The proportion of mature females per 1 mm CL size-class rose logistically with CL in both data sets (Figure 4A,B). The size at which 50% was mature (CL_{50}) was estimated to be 15.37 mm CL for proportion of females with maturing and mature ovaries and 16.49 mm CL for proportion of inseminated females (Figure 4A,B). No difference in CL_{50} between the two categories was found in 95% confidence limit. Ovarian maturity gives an overestimate of the size of maturity, since spent ovaries are classed as immature. The statistical analysis also revealed that the distribution of mature proportions between the two different methods was not significantly different (Kolmogorov–Smirnov two-sample test: $D_{max}=0.231$, $P>0.8$). Ovarian maturity

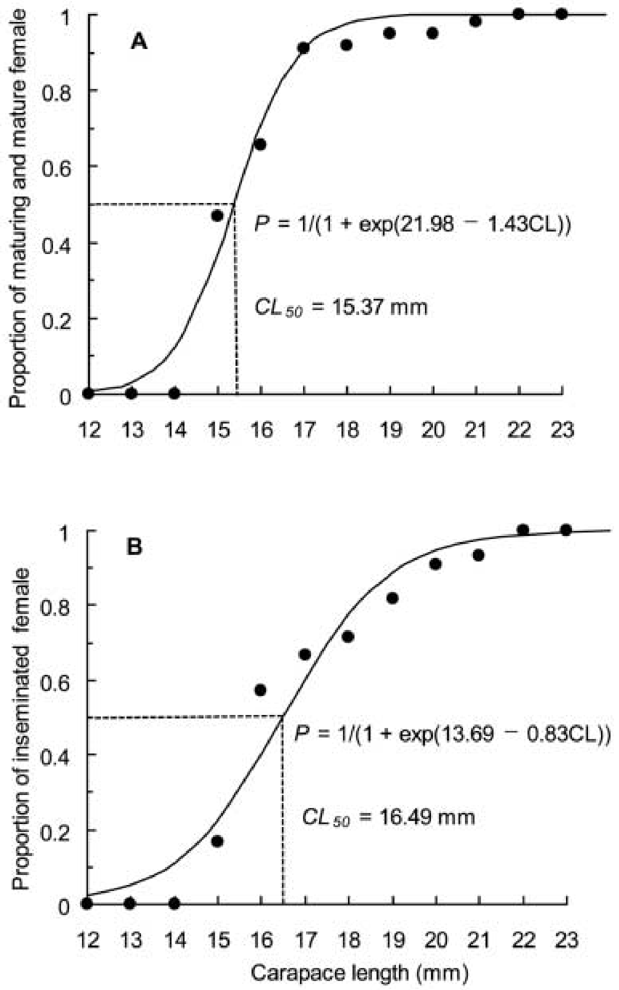

Figure 4. *Trachysalambria curvirostris*: logistic functions fitting (A) the cumulative proportion of maturing and mature female, and (B) the cumulative proportion of inseminated female. CL_{50}, which corresponds to each proportion of 0.5 (50% of females are mature), is indicated.

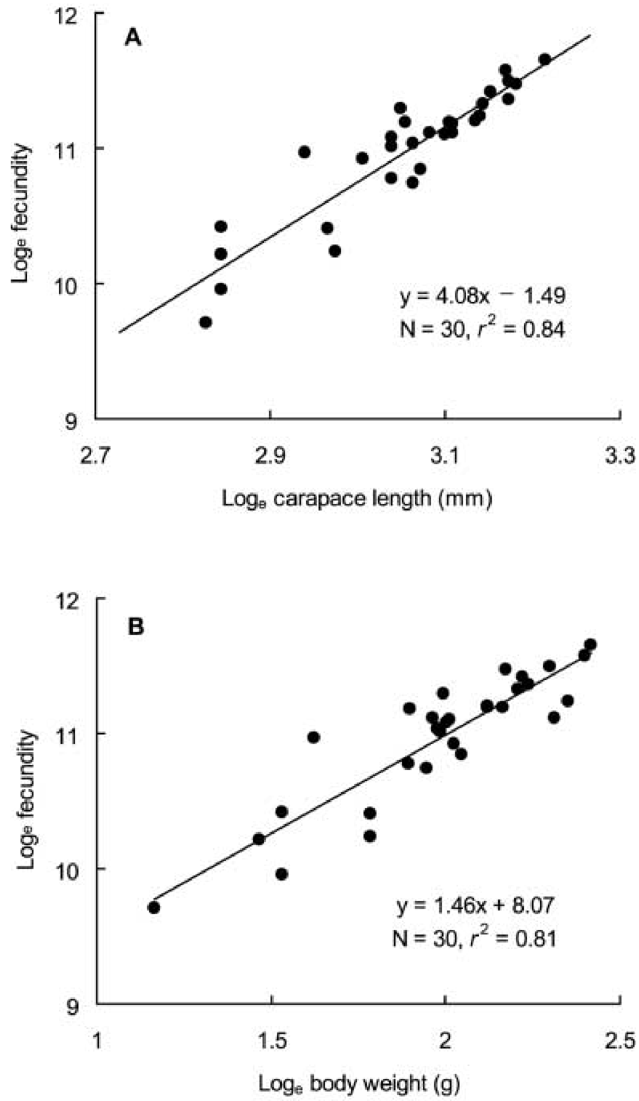

Figure 5. *Trachysalambria curvirostris*: regressions of $\log_e$ fecundity on $\log_e$ carapace length (mm) (A), and on $\log_e$ body weight (g) (B).

may overestimate the size at sexual maturity, since females with spent ovaries are categorized as immature. Thus the proportion inseminated could provide a better index.

The observed fecundity varied between 16,380 eggs at 16.5 mm CL and 114,621 eggs at 24.9 mm CL. Regression analysis on natural logarithm transformed data showed a significant relationship between ova number (F) and CL: $\log_e F = 4.08$ (95% CL ± 0.34) $\log_e CL - 1.49$ ($N = 30$, $r^2 = 0.84$, $P < 0.001$) (Figure 5A). The relationship between ova number (F) and BW was also significant: $\log_e F = 1.46$ (95% CL ± 0.13) $\log_e BW + 0.87$ ($N = 30$, $r^2 = 0.81$, $P < 0.001$) (Figure 5B). The slopes of the two regressions were just significantly greater than 3.0 or 1.0 at a 95% confidence limit of slope, indicating a significantly positive allometry.

Growth

Population structure of the cocktail shrimp was similar between the two years and statistical analysis revealed no significant difference in the population size–frequency distribution between the two years (Kolmogorov–Smirnov two-sample test, $P > 0.1$). Length–frequency distributions showed that both females and males showed two modal size groups per year (Figure 6), indicating apparent shift in modal length with time. The life span of females appeared to be 14–15 months according to size–frequency distributions, while that of the male was 13–14 months. The small newly-spawned shrimps appearing as a new cohort in June grew so rapidly to December, migrated offshore and began to grow in April when the inshore migration occurred along with the increased water temperature. In females, the sample in April 1994 was essentially unimodal, with a mean of 18.1 mm CL. This mode could be followed through to August 1994, when this group grew to a mean of 22.3 mm CL. Based on the spawning peak and plankton survey mentioned above, the second mode appeared to be formed by a new cohort spawned in June 1994. Based on the plankton survey (Table 1) the mean CL of the cohort at this time is assumed as 0.36 mm CL. This group had a mean of 14.6 mm CL and could be traced through to July 1995. Males displayed similar modal progression.

The VBGF parameters for each sex were estimated using a mean CL at age. The modal progression analysis

https://doi.org/10.1017/S0025315404009270h Published online by Cambridge University Press

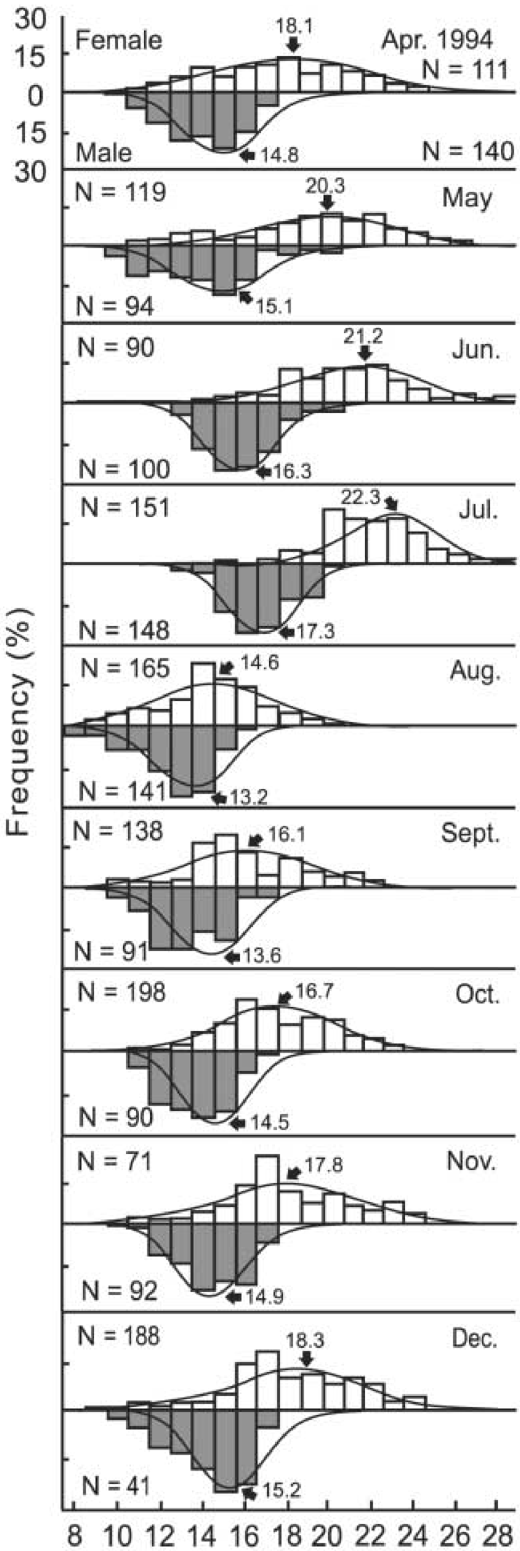

Figure 6. *Trachysalambria curvirostris*: length–frequency distribution for specimens sampled monthly between April 1994 and November 1995. Curves and arrows indicate normal distributions of cohorts and their means, respectively.

for each sex separately showed that females had higher L_∞ than males and K values of both sexes the same (L_∞=24.64 mm CL and K=2.00 y^{-1} for females, and L_∞=19.00 mm CL and K=2.00 y^{-1} for males). The growth performance indices (ϕ') showed that females (3.08) were higher than males (2.86). This indicates that females had greater growth rates at age than males (Figure 7). The amplitude of seasonal growth oscillates so strongly (C>1), suggesting the sustained periods of non-growth, such as could occur in the over-wintering period of the shrimps. The phase of slow growth (WP) was January for both females and males.

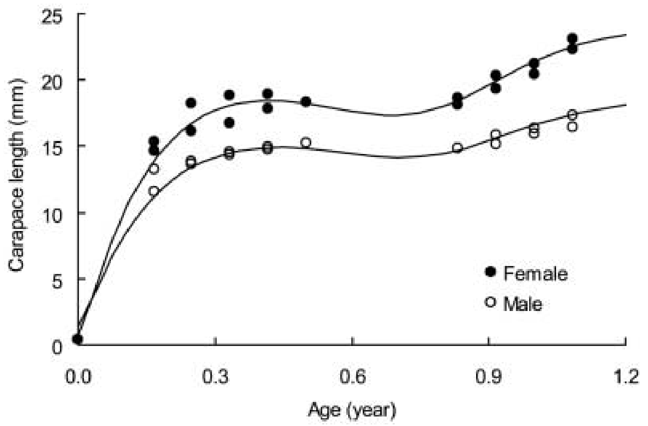

Figure 7. *Trachysalambria curvirostris*: seasonalized growth curves for females and males based on the modified VBGF parameters. The flat areas of the curve indicate reduced growth rates during over-wintering periods.

DISCUSSION

One of the most interesting aspects is the reason for the striking success of *Trachysalambria curvirostris* on the western coast of Korea in contrast to the eastern coast of Korea. The western coast of Korea has relatively shallow waters with a maximum depth of little over 30 m in each case. This species is caught mainly by the inshore fishery, and not by the deeper fishery. This suits the requirements of *T. curvirostris*, which is generally regarded as a shallow water species. In the present study, specimens were abundant in shoreline catches from shallow areas.

Sex ratio showed seasonal variations with the females predominating in the samples. Since females of this species are larger than males, this could be partly due to selectivity of collecting gear.

The bionomics of *T. curvirostris* in Korea can be compared with other areas. In the present study, the maximum size recorded was 28.9 mm CL (TL 101.4 mm) for females, and 20.5 mm CL for males. In the Suez Canal, the maximum size recorded was about 22.2 mm CL (TL 93.0 mm) for females (Gab-Alla et al., 1990), less than in Korea. However in the open Pacific Ocean females reach 108 mm TL (Ueta, 1987). In the present study, the life span of females was 14–15 months, and that of males 13–14 months. However in the Kii Channel, Japan, the life span of females and males were both 12–19 months (Ueta, 1987), and in the Sendai Bay females and males were two years and one year, respectively (Kosaka, 1979). It is most likely that these differences are primary consequences of geographical differences.

The spawning season of *T. curvirostris* in Korea extended from early June to August, as reflected by both the incidence of mature females, and the occurrence of larvae in the plankton. This is slightly shorter than that reported in the Kii Channel, Japan, where spawning began in May and continued through to October (Sakamoto & Hayashi, 1977). The occurrence of two major spawning periods is common in *T. curvirostris* in the Kii Channel, Japan (Sakamoto & Hayashi, 1977). In the present study, female GSI reached a peak in June/July, then after spawning it began to decrease from August. This pattern suggests that this species has one peak of spawning activity. The smallest mature females in Korea were 15 mm CL, and the size at sexual maturity (CL_{50}), was estimated at 15.37 mm CL for mature females and at 16.49 mm CL for inseminated females. In contrast, in the Suez Canal Gab-Alla et al. (1990) estimated the minimum size of female maturity as 9 mm CL, and size at 50% maturity as 19 mm CL. It is most likely that these differences are primarily affected by environmental factors, particularly water temperature.

Some studies suggested the possible source of error in the size at sexual maturity of penaeid prawns. Garcia (1985) noted that the proportion of mature females is a biased index of population reproduction. For some penaeids in the Suez Canal, Gab-Alla et al. (1990) also suggested that since spent ovaries are categorized as immature, ovarian maturity may lead to an overestimate of the size of maturity, and thus that the proportions of inseminated females could be a better index of female maturity. In the present study, however, any significant difference in CL_{50} between ovarian maturation and insemination methods was not found. This result suggests that in *T. curvirostris* insemination may be closely related to ovarian maturation, as observed in *Penaeus japonicus* Bate, 1888 and *Penaeus chinensis* (Chu, 1995; Cha et al., 2002).

The percentage of inseminated females and GSI both showed the same seasonal pattern. This pattern suggests that insemination is clearly related to the stage of ovarian maturation. For most species of penaeid shrimps females spawn offshore and the larvae gradually migrate inshore as postlarvae (Dall et al., 1990). In the present study, a high proportion of mature females and males were sampled during the reproductive season close to the coast. This suggests that *T. curvirostris* matures and mates inshore, near the coast. Therefore, unlike many other penaeids, this species does not depend to the same extent on an offshore migration to deeper water for breeding. Results of the present study show that the life cycle of *T. curvirostris* does involve migration, though much more limited in range.

The larval distributions described in this study correspond to adult distributions, based on catches for *T. curvirostris* around Poryoung areas. The larval distribution and abundance are also useful for predicting adult distribution and abundance in areas that have not been sampled. Large numbers of *T. curvirostris* larvae have been found between Kanghwado and Poryoung for example. Such results could also be used to increase the resolution of fisheries logbook data. The reproductive dynamics, as inferred from larval abundance, agree quite closely with surveys of adults. The spawning season, as assessed by larval abundance, occurs in the summer season: June–August.

In the present study there is an apparent shift in modal length with time in both females and males during the two years. A cohort spawned in June continued to grow through to the following summer and took part in spawning in next June–July. After that, they started to die. Recruitment to the fished population took place in August and is compatible with a one year life cycle. These patterns were also found in numerous penaeids around this study area (Pauly et al., 1984; Choi, 2001; Cha et al., 2002). This study indicated that *T. curvirostris* underwent one major recruitment event per year. Recruitment followed a single reproductive period from June to July and recruits were found in adult catches as a clearly distinguishable cohort in August. The recruitment of pre-adults is likely to take place within 1–2 months after spawning activity.

The modified von Bertalanffy growth models fitted the data of the *T. curvirostris* population of Korea well, as indicated from regression coefficients of nonlinear regression. The K values (2.0 in females and males), corresponding to the best estimate of L_∞ (24.64 in females and 19.0 in males) for both sexes. There are differences in the growth performance indices (ϕ') between the two sexes, indicating that females grew faster and reached a larger size at age than males. Although similar patterns of growth were found in numerous decapod shrimps (Pauly et al., 1984; Bergström, 1992; Cha, 1997; Oh et al., 1999), to date it is not clear why females of these species exceed males in growth rate. Slow growth of the both sexes occurred within the winter months of January. The slow growth phase coincided with overwintering periods when lower water temperature and subsequently food availability are prevailing. The amplitude of seasonal growth oscillates so strongly ($C>1$). This suggests the sustained periods of non-growth, such as could occur in the over-wintering areas of the shrimps. On the shrimp population, the seasonal growth oscillations correlate well with the intensity of the annual temperature fluctuation (Pauly et al., 1984).

We express our thanks to Dr R.G. Hartnoll and Dr Taisoo E. Park for critical reading and comments on the manuscript. This work was carried out as part of the National Fisheries Research and Development Institute Project.

REFERENCES

Bergström, B., 1992. Growth, growth modeling and age-determination of *Pandalus borealis*. *Marine Ecology Progress Series*, **83**, 167–183.

Cha, H.K., 1997. *Ecology of* Metapenaeus joyneri *Miers and* Trachypenaeus curvirostris *Stimpson (Decapoda: Penaeidae) in the western coast of Korea*. PhD thesis, Pukyong National University, Busan, Korea.

Cha, H.K., Oh, C.W., Hong, S.Y. & Park, K.Y., 2002. Reproduction and population dynamics of *Penaeus chinensis* (Decapoda: Penaeidae) on the western coast of Korea, Yellow Sea. *Fisheries Research*, **56**, 25–36.

Choi, J.H., 2001. *Growth and reproductive biology of* Metapenaeopsis dalei *(Decapoda: Penaeidae) in the Korean waters*. PhD thesis, Pukyong National University, Busan, Korea.

Chu, K.H., 1995. Aspects of reproductive biology of the shrimp *Metapenaeus joyneri* from the Zhujiang estury, China. *Journal of Crustacean Biology*, **15**, 214–219.

Dall, W., Hill, B.J. & Staples, D.J., 1990. The biology of the Penaeidae. In *Advances in Marine Biology*, vol. 27 (ed. J.H.S. Blaxter and A.J. Southward), pp. 1–461. San Diego: Academic Press.

Gab-Alla, A.A., Hartnoll, R.G., Ghobashy, A.F. & Mohammed, S.Z., 1990. Biology of penaeid prawns in the Suez Canal lakes. *Marine Biology*, **107**, 417–426.

Garcia, S., 1985. Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations. In *Proceedings of the Second Australian National Prawn Seminar* (ed. P.C. Rothlisberg et al.), pp. 139–158. Australia: NPS2.

Holthuis, L.B., 1980. FAO species catalogue. Vol. 1. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis No. 125*, **1**, 1–261.

Kim, H.S., 1977. *Illustrated encyclopedia of flora and fauna of Korea*. Seoul: Samhwa Publication Company.

Kim, Y.H., Lee, S.D. & Kim, B.G., 1984. Ecological study on the shrimp, *Trachypenaeus curvirostris*. *Korea Bulletin of National Fisheries Research Development and Institute*, **32**, 25–30.

Kosaka, M., 1979. Ecological notes on the penaeid shrimp, *Trachypenaeus curvirostris* (Stimpson), in Sendai Bay. *Bulletin of the Faculty of Fisheries of Tokai University*, **12**, 167–172.

Oh, C.W., Hartnoll, R.G. & Nash, R.D.M., 1999. Population dynamics of the common shrimp, *Crangon crangon* (L.), in Port Erin Bay, Isle of Man, Irish Sea. *ICES Journal of Marine Science*, **56**, 718–733.

Pauly, D. & Gaschütz, G., 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM 1979/G:24, 26 pp.

Pauly, D., Ingles, J. & Neal, R., 1984. Application to shrimp stocks of objective methods for the estimation of growth, mortality and recruitment-related parameters from length-frequency data (ELEFAN I and II). In *Penaeid shrimps—their biology and management* (ed. J.A. Gulland and B.J. Rothschild), pp. 220–234. Surrey: Fishing News Books.

Pauly, D. & Munro, J.L., 1984. Once more on the comparison of growth in fish and invertebrates, *Fishbyte*, **2**, 21.

Ronquillo, J.D. & Saisho, T., 1995. Developmental stages of *Trachypenaeus curvirostris* (Stimpson, 1860) (Decapoda, Penaeidae) reared in the laboratory. *Crustaceana*, **68**, 833–863.

Sakamoto, T. & Hayashi, K., 1977. Prawns and shrimps collected the Kii Strait by small type trawlers. *Bulletin of the Japanese Society of Scientific Fisheries*, **43**, 1259–1268.

Sokal, R.R. & Rohlf, F.J., 1995. *Biometry. The principles and practice of statistics in biological research*, 3rd edn. San Francisco: W.H. Freeman & Company.

Ueta, Y., 1987. Reproduction and growth of *Trachypenaeus curvirostris* (Penaeidae, Decapoda, Crustacea) in Kii Channel. *The Suisanzoshoku*, **35**, 161–169.

Submitted 2 February 2003. Accepted 21 February 2004.