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## POPULATION BIOLOGY OF THE SWIMMING CRAB *PORTUNUS SANGUIOLENTUS* IN THE WATERS OFF NORTHERN TAIWAN

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### ABSTRACT

The growth, mortality, and reproduction of *Portunus sanguinolentus* were studied using size-frequency data obtained from crabs collected in pots in the waters off northern Taiwan from October 2000 to March 2001, and October 2001 to January 2002. The Bhattacharya's method and seasonal von Bertalanffy growth curve were used to estimate growth parameters. The growth curve for males was  $L_t = 204.75 \times \{1 - e^{-[0.87t + 0.4(0.87/2\pi)\sin 2\pi(t)]}\}$  and the curve for females was  $L_t = 194.25 \times \{1 - e^{-[0.97t + 0.4(0.97/2\pi)\sin 2\pi(t)]}\}$ . A size-converted catch curve was used to estimate the instantaneous total mortality rate (Z), and Pauly's empirical equation was used to estimate the instantaneous natural mortality rate (M). For males,  $Z = 3.16/\text{year}$  and  $M = 1.65/\text{year}$ . For females,  $Z = 3.37/\text{year}$  and  $M = 1.8/\text{year}$ . The instantaneous fishing mortality rate (F) was 1.51/year and 1.57/year, and the exploitation rate (E) was 0.48 and 0.47 for males and females, respectively. The exponential relationships were presented for relationships of fecundity in number and weight of egg mass in terms of carapace width and body weight. Those relationships were statistically significant ( $P < 0.01$ ), indicating that the fecundity increased with the size from  $4.05 \times 10^5$  to  $2.44 \times 10^6$  eggs.

The swimming crab *Portunus sanguinolentus* (Herbst, 1783) is widely distributed in ocean waters from East Africa, through the Indo-Pacific region, to the Hawaiian Islands (Stephenson and Campbell, 1959). Juveniles and adult males typically inhabit sandy and muddy bottoms in nearshore waters, about 10–30 m deep (Chapgar, 1957; Sumpton *et al.*, 1989). In contrast, females are abundant in 40–80 m depths (Wenner, 1972; Campbell and Fielder, 1986). In Taiwan, *P. sanguinolentus* only occurs in the waters around the north and southwest parts of the island.

There have been numerous studies of *P. sanguinolentus* taxonomy (Chapgar, 1957; Stephenson and Campbell, 1959; Dai and Yang, 1991), maturation (Sumpton *et al.*, 1989; Jacob *et al.*, 1990; Reeby *et al.*, 1990), and reproduction (Ryan, 1967; Campbell and Fielder, 1986; Sukumaran and Neelakantan, 1997). However, there has been only little information about *P. sanguinolentus* in the waters of Taiwan (Huang, 1993; Hsu *et al.*, 2000). The yield of this economically important and productive species has declined substantially in recent years (Anonymous, 2000), and the monthly relative abundance also shows a declining trend (unpublished data). To understand the population dynamics of *P. sanguinolentus* around Taiwan is urgent, and locally collected data

used to study its growth, mortality, and reproduction are needed.

In this paper, growth study was performed to estimate growth parameters and to understand the life span. Then, mortality was estimated to understand causes of population reduction. Finally, fecundity was estimated based on carapace width and body weight to determine recruitment. Therefore, the objective of this study was to estimate growth, mortality, and reproduction of *P. sanguinolentus* living in the waters off northern Taiwan.

### MATERIALS AND METHODS

From October 2000 to March 2001, and October 2001 to January 2002, monthly samples of *P. sanguinolentus* were collected using circular crab pots in the offshore waters of northern Taiwan ( $25^{\circ}20' - 25^{\circ}50'N$  and  $120^{\circ}40' - 121^{\circ}20'E$ ). Pot is made of a rigid frame (diameter is 550 mm and height is 240 mm) with meshes (upper mesh size is 35 mm and lower mesh size is 40 mm) and three entrances are inserted on the side (mesh size of entrance is 15 mm). The entrances are designed to prevent crabs escaping. Before setting, pots are baited with frozen mackerels in the center of the pot.

Basic hydrographic data were obtained from the National Center for Oceanic Research database (National Taiwan University, Taipei, Taiwan). In the study area, the water depth was around 80 m, and the substrate was sandy. Bottom temperatures ranged from  $20 \pm 0.29^{\circ}C$  in winter to  $25 \pm 1.53^{\circ}C$  in summer. The annual average temperature was  $23 \pm 3.2^{\circ}C$ , and salinity averaged  $34 \pm 0.39$  psu (practical salinity units).

Nearly all crabs captured in each pot were identified, sexed, and measured for carapace width (CW). Precision

vernier calipers were used in the field to measure CW (the distance from the left tip to the right tip of the posterior margin of the carapace) to the nearest 0.01 mm (Mitutoyo digimatic caliper). Each month, from October 2000 to March 2001, 20 gravid females were selected and brought to the laboratory to study reproduction. During the main spawning season, from October 2001 to January 2002, the number of gravid females in each sample was counted. Altogether, 3298 females and 1504 males were measured, and 117 gravid females with extruded eggs were collected and frozen.

Prior to measuring, each frozen, gravid female was thawed for about 4 h in the laboratory. For each crab, the CW was measured as described above. The wet weight of body, with eggs, was determined to the nearest 0.1 gram with an electronic balance (Snowrex digital scale KF-600). Then the eggs were carefully removed from the pleopods, wiped with tissue paper, and weighed. To maintain tonicity (Wenner *et al.*, 1987) for measurements, eggs were preserved in a mixture of 30% water, 30% ethanol, 30% acetone, and 10% glycerol.

### Growth

First, the ELEFAN I subroutine of the FiSAT software package (Gayaniilo and Pauly, 1997) was used to estimate a seasonalized version of the von Bertalanffy growth parameters. The growth model with a seasonal fluctuation is:

$$L_t = L_\infty \left\{ 1 - e^{-K \times (t - t_0) + C \times (K/2\pi) \times \sin 2\pi(t - t_s)} \right\}, \quad (1)$$

where  $L_t$  (mm) is the predicted length at time  $t$ ,  $L_\infty$  (mm) is the asymptotic length,  $t$  is a given instant age,  $t_0$  is the theoretical age when carapace width is zero,  $t_s$  is the starting point of the growth oscillation,  $K$  (1/year) is the intrinsic growth rate,  $C$  is the amplitude of the growth oscillation and ranges from 0 to 1. The growth performance index ( $\phi'$ ) was used to compare von Bertalanffy growth of *P. sanguinolentus* with that of other crab species, in which  $\phi' = \log K + \log L_\infty$  (Pauly and Munro, 1984). Then, Bhattacharya's method was used to determine the number of age groups in monthly samples (Bhattacharya, 1967).

Hottelling's  $T^2$ , calculated with the SAS/IML module, was used to compare male and female growth curves based on the parameters  $L_\infty$ ,  $K$ ,  $C$ ,  $t_s$ , and  $t_0$  (Bernard, 1981; Quinn and Deriso, 1999). When the  $T^2$  statistic was significant, indicating the growth of males and females was significantly different, simultaneous Roy-Bose confidence intervals were computed to determine the most important parameter causing the difference between the sexes (Bernard, 1981).

### Mortality

The instantaneous total mortality rate ( $Z$ , 1/year) was estimated based on the size-converted catch curve (King, 1995) using seasonal von Bertalanffy growth parameters:

$$\ln \left( \frac{N_i}{\Delta t} \right) = \alpha + \beta \cdot t_i, \quad (2)$$

where  $N_i$  is the number of individuals of size class  $i$ ,  $\Delta t$  is the time needed to grow through size class  $i$ ,  $t_i$  is the relative age of size class  $i$ ,  $\alpha$  and  $\beta$  are parameters to be estimated. Thus, the instantaneous total mortality rate is  $Z = -\beta$ .

The instantaneous natural mortality rate ( $M$ , 1/year) was estimated with Pauly's empirical equation (Pauly's, 1980):

$$\ln(M) = -0.0152 - 0.279 \ln(L_\infty) + 0.6543 \ln(K) + 0.463 \ln(T), \quad (3)$$

where  $\ln$  is the natural logarithm operator;  $L_\infty$  (cm) and  $K$  (1/year) are growth parameters (described above) and  $T$  ( $^{\circ}\text{C}$ ) is

the mean annual habitat temperature. Thus, the instantaneous rate of fishing mortality ( $F$ , 1/year) is  $F = Z - M$ , and the exploitation rate ( $E$ ) is  $E = F/Z$  (Quinn and Deriso, 1999).

### Reproduction

The proportion of gravid females, which were used as mature females, was fitted to a logistic equation as described by Quinn and Deriso (1999):

$$P(L) = \frac{P_{\max}}{1 + e^{-\kappa \times (L - \gamma)}}, \quad (4)$$

where  $P(L)$  is the cumulative proportion of gravid females in CW upper class limit ( $L$ ) and  $\kappa$ ,  $\gamma$ , and  $P_{\max}$  are parameters estimated by the log-linear least square method (Zar, 1995).  $P_{\max}$  is the asymptotic cumulative proportion of gravid females as  $L \rightarrow \infty$ ,  $\kappa$  is the curvature, and  $\gamma$  is the CW at the inflection point.

Before pooling all the monthly data to fit equation (4), a Kruskal-Wallis' one-way analysis of variance (SAS, Version 8.02) was used to examine the randomness of the monthly data, which were assumed to be from one population. The proportion of gravid females did not vary significantly from month to month ( $\chi^2_{(0.05,3)} = 0.547$ ,  $P > 0.05$ ). Therefore, we assumed all samples were randomly collected from the same population, and all monthly samples were combined by size intervals to fit the logistic curve (equation 4).

The gravimetric method was used to estimate number of newly deposited eggs extruded by gravid females. The diameters of 30, randomly selected eggs were measured. The relationships between the number of eggs or the weight of the extruded eggs and female carapace width or weight can be expressed by:

$$Y = \alpha \cdot X^\beta, \quad (5)$$

where  $Y$  denotes either the number of eggs or the weight of the eggs;  $X$  is either carapace width or the body weight of the female crab from whence the eggs came; and  $\alpha$  and  $\beta$  are estimated parameters.

## RESULTS

### Growth

The von Bertalanffy growth equations with seasonal fluctuations (Fig. 1) were:

$$(1) \text{ Males: } L_t = 204.75 \times \left\{ 1 - e^{-[0.87t + 0.4(0.87/2\pi) \sin 2\pi(t)]} \right\} \quad (\phi' = 2.25); \quad (6)$$

$$(2) \text{ Females: } L_t = 194.25 \times \left\{ 1 - e^{-[0.97t + 0.4(0.97/2\pi) \sin 2\pi(t)]} \right\} \quad (\phi' = 2.28), \quad (7)$$

$L_\infty$  and  $K$  were the only parameters that differed between sexes. Female growth rate ( $K = 0.97/\text{year}$ ) was greater than male growth rate ( $K = 0.87/\text{year}$ ), but males reached a larger asymptotic size (204.75 mm) than females (194.25 mm).  $L_\infty$  and  $K$  were significantly negatively correlated (males:  $r = -0.826$ ,  $P < 0.01$ ;

females:  $r = -0.787$ ,  $P < 0.01$ ). Thus, females reach maximum size in less time than males. Furthermore, the results obtained by Bhattacharya's method indicated almost all monthly samples might include two age-classes, and the longevities of male and female *P. sanguinolentus* are asymptotically over 11.4 and 10.2 years, respectively, corresponding to the asymptotic carapace widths ( $L_\infty$ ) in growth equations (6) and (7), respectively.

Hence, to determine whether the growth rates and asymptotic sizes of male and female *P. sanguinolentus* differed, the test statistic, Hotelling's  $T^2$  (Bernard, 1981), was computed. Female and male  $L_\infty$  and  $K$  were significantly different (reject  $H_0: \Theta_{(female)} = \Theta_{(male)}$ ,  $P < 0.01$ ; Table 1). However, the 99% Roy-Bose confidence interval for  $K_{(female)} - K_{(male)}$  indicated that  $K$  is not significantly different between sexes, but the 99% confidence interval for  $L_{\infty(female)} - L_{\infty(male)}$  is different between sexes. In conclusion, females do not grow significantly faster than males, but they do achieve their maximum size, which is significantly smaller than the maximum size of males, in significantly less time (CW range: males 90–193 mm and females 68–182 mm).

Mortality

Based on the carapace width-frequency distribution (Table 2), the size-converted catch

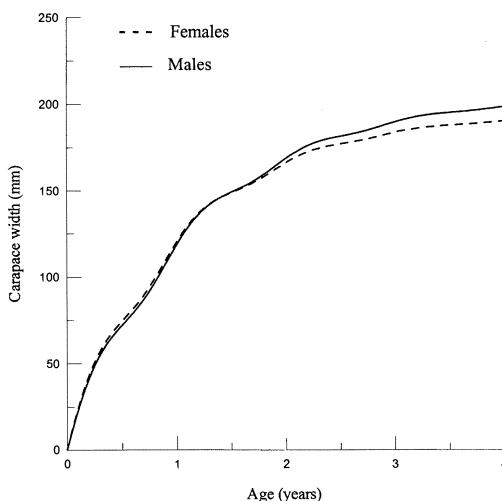


Fig. 1. Seasonal von Bertalanffy growth curves based on carapace width frequency data for male (—) and female (---) *P. sanguinolentus*.

curve was used to estimate instantaneous total mortality for both sexes (Fig. 2). The instantaneous total mortality rate ( $Z$ ) was 3.16/year for males and 3.37/year for females. Using Pauly's empirical equation and an average annual habitat temperature of 23°C, the natural mortality rate ( $M$ ) was 1.65/year for males and 1.8/year for females. The fishing mortality rate ( $F$ ) was 1.51/year for males and 1.57/year for females, and the exploitation rate ( $E$ ) was 0.48

Table 1. Hotelling's  $T^2$  calculation to test for equality of parameters  $L_\infty$  and  $K$  for male and female *P. sanguinolentus* in the waters off northern Taiwan.  $H_0: \Theta_{(female)} = \Theta_{(male)}$  versus  $H_1: \Theta_{(female)} \neq \Theta_{(male)}$ .

Parameters	Female	Male
$L_\infty$	194.25	204.75
$K$	0.97	0.87
Correlation matrix	$\begin{bmatrix} 1 & -0.787 \\ -0.787 & 1 \end{bmatrix}$	$\begin{bmatrix} 1 & -0.826 \\ -0.826 & 1 \end{bmatrix}$
Variance-covariance matrix	$\begin{bmatrix} 8887.949 & -179.579 \\ -179.579 & 5.861 \end{bmatrix}$	$\begin{bmatrix} 15623.171 & -192.126 \\ -192.126 & 3.462 \end{bmatrix}$
Pooled variance-covariance matrix	$\begin{bmatrix} 10996.916 & -183.508 \\ -183.508 & 5.110 \end{bmatrix}$	
$\Delta\Theta = \begin{bmatrix} L_\infty \\ K \end{bmatrix}_{female} - \begin{bmatrix} L_\infty \\ K \end{bmatrix}_{male}$	$\begin{bmatrix} -10.5 \\ 0.1 \end{bmatrix}$	
	$F_{0.01,2,4799} = 6.604 > F_{0.01,2,\infty} = 4.605$ $T_{0.01,2,4799}^2 = 13.210 > T_{0.01,2,\infty}^2 = 5.991$	Conclusion: reject $H_0$ Critical F 3.554
Roy-Bose intervals (99% CI)	$-20.403 \leq L_{\infty(female)} - L_{\infty(male)} \leq -0.597$ $-0.113 \leq K_{(female)} - K_{(male)} \leq 0.313$	0.694

Table 2. Size-converted catch curves for male (upper panel) and female (lower panel) *P. sanguinolentus* based on carapace width frequency data.

Carapace width CW <sub>1</sub> -CW <sub>2</sub> (mm)	Mid CW (mm)	Number	Age (t) at CW <sub>1</sub> (years)	Age (t) change (years)	Age (t) at mid CW (years)	ln(N/Δt)
<b>Males</b>						
85-95	90	2	0.673	0.107	0.726	2.932
95-105	100	29	0.779	0.093	0.826	5.741
105-115	110	180	0.873	0.090	0.918	7.596
115-125	120	307	0.963	0.098	1.012	8.055
125-135	130	235	1.060	0.120	1.120	7.582
135-145	140	236	1.180	0.189	1.275	7.132
145-155	150	278	1.369	0.316	1.527	6.781
155-165	160	162	1.684	0.232	1.800	6.548
165-175	170	61	1.917	0.246	2.040	5.512
175-185	180	10	2.163	0.659	2.513	2.659
185-195	190	4	2.752	0.743	3.102	1.743
<b>Females</b>						
65-75	70	4	0.375	0.130	0.440	3.426
75-85	80	23	0.505	0.138	0.574	5.115
85-95	90	23	0.643	0.113	0.699	5.317
95-105	100	111	0.756	0.097	0.804	7.044
105-115	110	496	0.853	0.093	0.899	8.582
115-125	120	609	0.946	0.100	0.996	8.716
125-135	130	650	1.046	0.123	1.107	8.572
135-145	140	660	1.169	0.199	1.268	8.108
145-155	150	500	1.367	0.343	1.539	7.285
155-165	160	178	1.710	0.256	1.838	6.546
165-175	170	39	1.966	0.361	2.146	4.684
175-185	180	5	2.326	-2.326	1.163	1.864

for males and 0.47 for females. To determine total mortality rate ( $Z$ ) of male and female *P. sanguinolentus* differed, the analysis of covariance (ANCOVA) using age as the covariate revealed that there is a statistically significant difference ( $P < 0.0001$ ). Accordingly, total mortality rates were higher for females than males.

### Reproduction

Based on the female proportion in the population (the number of females in total catch) estimated from monthly samples, nearly all crabs caught in February and March were female (Fig. 3). Carapace width ranged from 90 mm to 193 mm for males and from 68 mm to 182 mm for females (Fig. 4). From 20% to 30% of the females caught each month were gravid and had extruded eggs (Fig. 4). The monthly sex ratio (the number of females divided by the number of males) was tested using  $\chi^2$  test, and the value was highly significant ( $\chi^2 = 1300.54 > \chi^2_{0.0001,10} = 35.557$ ) to reject the null hypothesis that the sex ratio is 1:1.

The proportion of gravid females among monthly samples was not significantly different (Kruskal-Wallis,  $\chi^2_{0.05,3} = 0.547$ ,  $P > 0.05$ ).

Therefore, the samples were pooled and a logistic curve (Fig. 5) was:

$$P(L) = \frac{1}{1 + e^{-0.141(L-135.27)}} \quad (8)$$

Further, the mean carapace width for ovigerous females ( $L_{50\%}$ ) was obtained as 135.27 mm from equation (8) assuming  $P(L) = 0.5$ .

The extruded egg mass was detached from the abdomen of each female, and the eggs were counted. The number of eggs ranged from 405,375 to 2,438,645 (average 1,075,857). Egg diameter ranged from 234  $\mu\text{m}$  to 297  $\mu\text{m}$ , with a mode of 270  $\mu\text{m}$  ( $n = 3420$ ). Additionally, the relationship between the number and weight of the eggs in each extruded egg mass were exponentially related to female carapace width and weight (Table 3). Egg number and weight were significantly positively correlated with body weight and carapace width ( $n = 117$ , each  $P < 0.01$ ).

## DISCUSSION

### Growth

In this study, seasonal fluctuation was incorporated into estimates of *P. sanguinolentus*

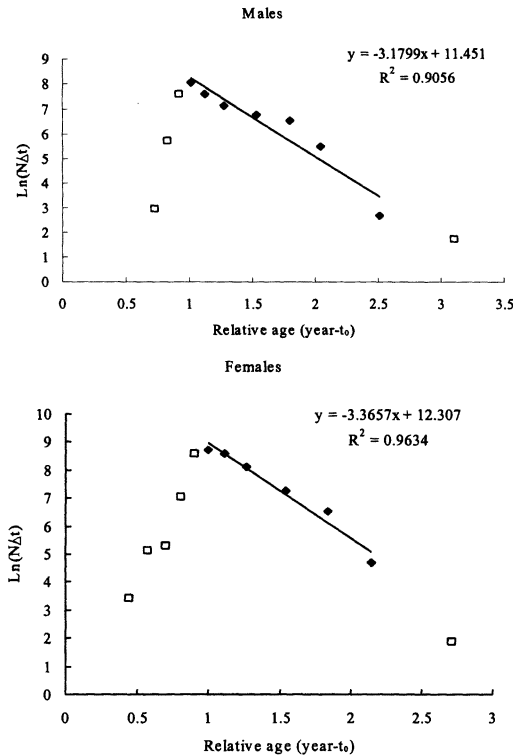


Fig. 2. Size-converted catch curves of male (upper panel) and female (lower panel) *P. sanguinolentus*. The total instantaneous mortality rates ( $Z$ ) were estimated from the slope of the regression line (solid squares); data points excluded in the regression line because of data from mean ages with very small sample size (less than 10) and the initial ascending data point representing groups of individuals which were not fully recruited (open squares). For males,  $Z = 3.155/\text{year}$  and for females,  $Z = 3.3657/\text{year}$ .

growth in the waters off northern Taiwan. Asymptotic carapace widths for males and females were estimated as 204.75 mm and 194.25 mm, respectively. These estimates are greater than those for *P. sanguinolentus* (163 mm and 173 mm for males and females, respectively) from waters off the southern Kanara Coast, India (Sukumaran *et al.*, 1986). However, estimated growth rates (males: 0.87/year; females: 0.97/year) in this study were much lower than those (3.54/year for both sexes) estimated by Sukumaran *et al.* (1986). The growth performance indexes for India population ( $\phi' = 2.76$  for males and 2.79 for females) were slightly greater than those of the present study, but both were located at the reasonable range ( $2 < \phi' < 3$ ) within the same family (Pauly and Munro, 1984). Defeo and Cardoso (2002) indicated that environmental factors, such as water temperature, may affect crab growth rate. Crab growth may be faster in warm water than in cool water (Leffler, 1972). As it is so, environmental differences may result in the discrepancies of growth of *P. sanguinolentus* from those two waters indicated above.

Growth rate differences between males and females result mainly from the greater reproductive output of females. When crabs become sexually mature, growth often decreases (Hartnoll, 1982) because of the significant amount of energy used for reproduction. In this study, the estimated  $L_{50\%}$  for females is 135.27 mm carapace width (about 1.17 years). After that, females grew slowly (Fig. 1) and seemed coincident with Hartnoll's points. With greater

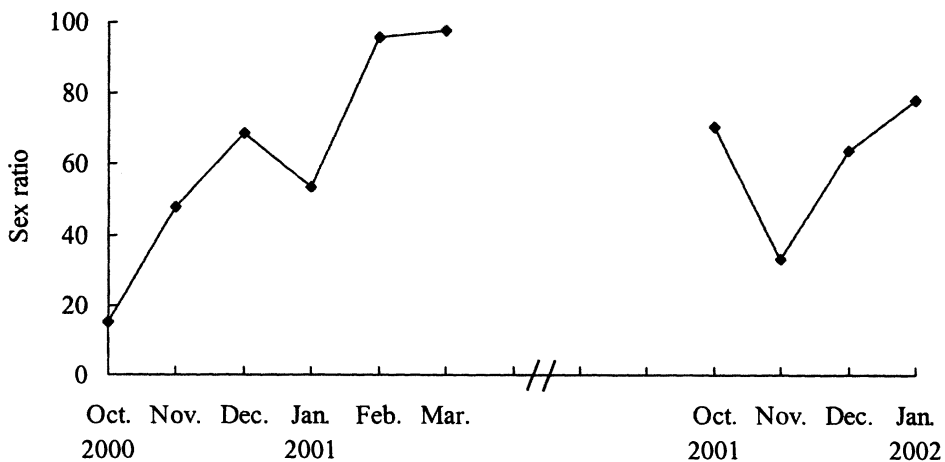


Fig. 3. Monthly change in the *P. sanguinolentus* female proportion in the population, October 2000 to January 2002.

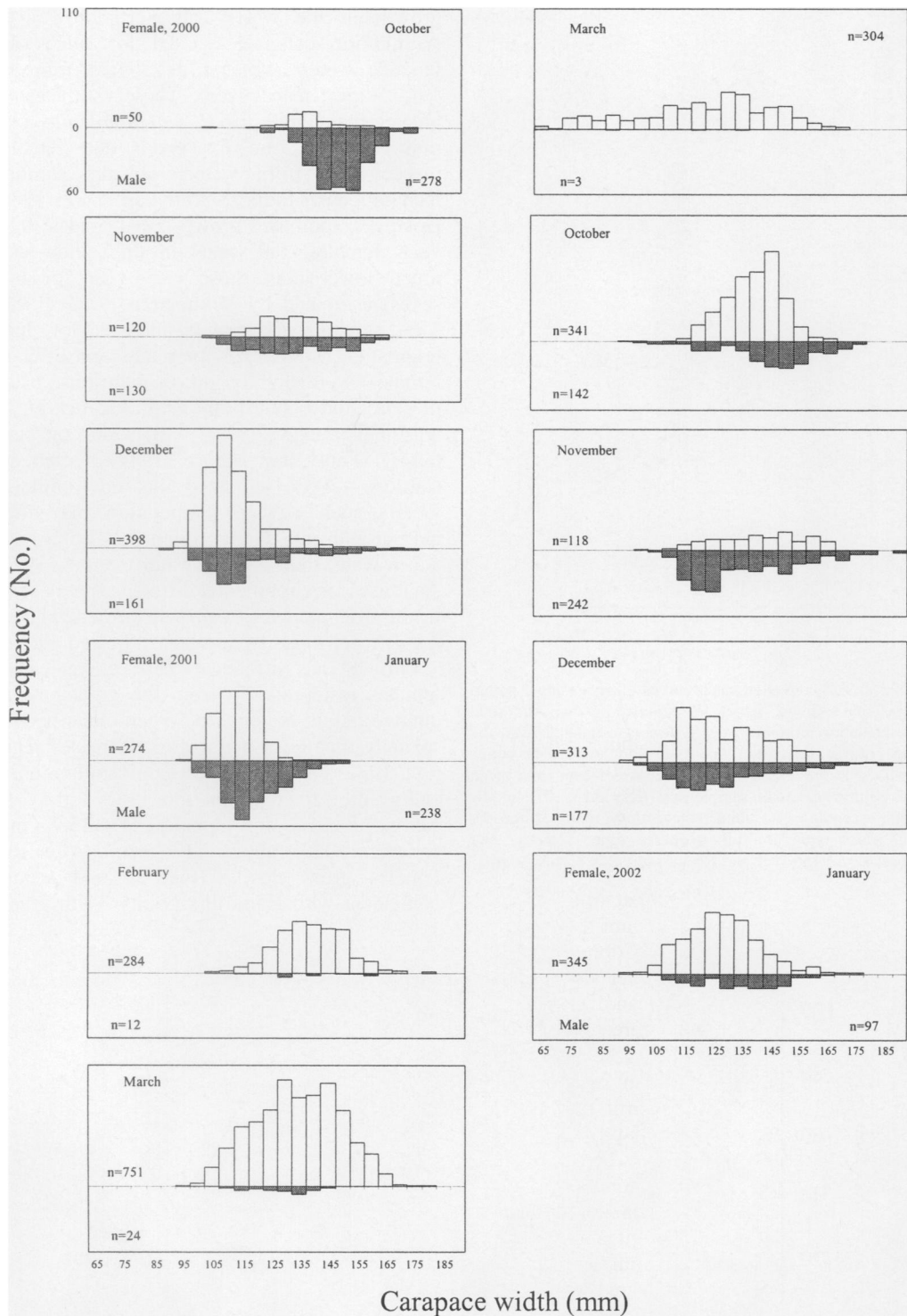


Fig. 4. The frequency distribution of carapace widths of male and female *P. sanguinolentus*. Solid squares denote gravid females and numbers indicate samples sizes of gravid females.

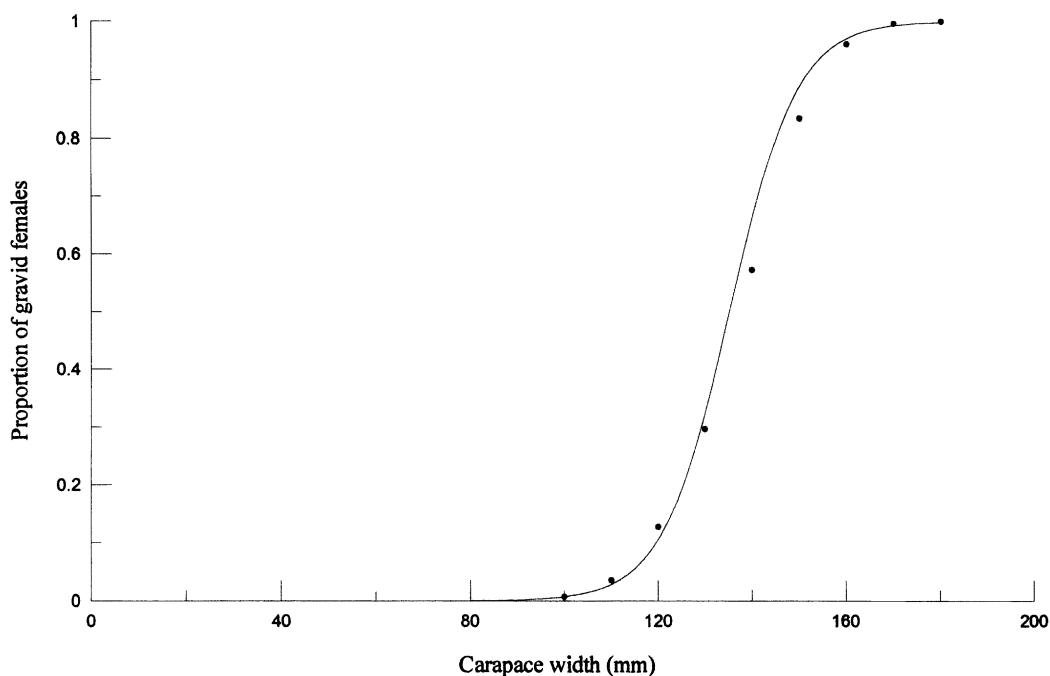


Fig. 5. A logistic curve of gravid female *P. sanguinolentus* and dotted line indicate the carapace width of proportion 0.5 corresponding to  $L_{50\%}$ .

investment in reproduction, females may be smaller than males at maturity. Reproductively active females typically postpone growth, and their growth rates often lag behind those of males (Cobb and Caddy, 1989). In this study, the asymptotic size of female *P. sanguinolentus* was smaller than that of males, and, overall, their growth was significantly slower. This supports the hypothesis that differences in reproductive output may account for differences in male and female growth (Cobby and Caddy, 1989; Hartnoll, 1982). However, the asymptotic size of females was larger than that of males in Indian population. This difference depends on the observed maximum carapace width due to the different sample location between Indian waters and the waters off North Taiwan.

Gayanilo and Pauly (1997) proposed that the maximum predicted size may be equivalent to 95% of the estimated asymptotic size. According to this viewpoint, the maximum predicted carapace width in the present analysis should be 194.5 mm and 184.5 mm for males and females, respectively, compared with the observed maximum carapace widths that were 193 mm and 182 mm CW for males and females, respectively, indicating that the present growth estimations and the corresponding predicted longevity are reasonable.

#### Mortality

Total mortality rates for *P. sanguinolentus* in the waters off northern Taiwan (males:  $Z = 3.16/\text{year}$ ; females:  $3.37/\text{year}$ ) were much greater than those obtained for *P. sanguinolentus* in the Indian Ocean (males:  $Z = 0.78/\text{year}$ ; females:  $0.79/\text{year}$ ; Sukumaran *et al.*, 1986). Part of these differences may be attributed to different methods of estimation and temperatures (Leffler, 1972). The exploitation rates (males:  $E = 0.48$ ; females:  $E = 0.47$ ) indicated that natural and fishing losses contributed equally to the decrease in the *P. sanguinolentus* population off northern Taiwan. During this study, *P. sanguinolentus* natural mortality was high. This is typical of r-selected species (Gunderson, 1980), which mature early and have high fecundity, short life spans, and small body size. However, these population traits may be affected by temperature and latitudinal variation (Defeo and Cardoso, 2002).

The size-converted catch curve is strongly influenced by population structure such as size at recruitment and sample size, which affect the goodness of fit and the slope of the regression line (cf. equation 2). There is no information about *P. sanguinolentus* recruitment to the crab pot fishery in the waters off Taiwan. Thus, the



Table 3. The percentage of gravid female *P. sanguinolentus* from October 2001 to January 2002 by carapace width class.

Carapace width class (mm)	October, 2001		November, 2001		December, 2001		January, 2001		Pooled	
	No.	Percent (%)	No.	Percent (%)	No.	Percent (%)	No.	Percent (%)	No.	Percent (%)
91–100	1	0.98	0	0	0	0	1	1.52	2	0.71
101–110	0	0	0	0	2	2.15	6	9.09	8	2.83
111–120	0	0	1	4.55	6	6.45	19	28.79	26	9.19
121–130	5	4.9	3	13.64	19	20.43	21	31.82	48	16.96
131–140	39	38.24	5	22.73	22	23.66	12	18.18	78	27.56
141–150	40	39.22	8	36.36	21	22.58	5	7.58	74	26.15
151–160	14	13.73	5	22.73	15	16.13	2	3.03	36	12.72
161–170	3	2.94	0	0	7	7.53	0	0	10	3.53
171–180	0	0	0	0	1	1.08	0	0	1	0.35

A Kruskal-Wallis test was used to assess the homogeneity of the percentage of gravid females across monthly samples:  $\chi^2(0.05, 3) = 0.5467$ , ( $P > 0.05$ , not significant)

total mortality rate was estimated for males and females separately based on carapace width frequency data (Table 2; Fig. 2), which were measured from all crabs caught during each trip to increase satisfactorily the sample size available in the present analysis.

#### Reproduction

In the monthly samples, female *P. sanguinolentus* outnumbered males. The inequality of female proportion in the population or sex ratio may result from the depth at which most samples were collected. Females were relatively more abundant around 80 m in depth, while males were more abundant from 40 m to 60 m. In addition, the proportion of females varied from year to year. This also was observed in the waters of Queensland, Australia (Sumpton *et al.*, 1989). Because the proportion of mature females increases significantly with increased depth (Wenner, 1972), offshore samples contain larger proportions of gravid females than samples from coastal areas.

For the Queensland population, Campbell and Fielder (1986) found that the female matured at 75 mm carapace width. Sumpton *et al.* (1989) found the smallest mature male and female were 83 mm and 74 mm carapace width, respectively, and the smallest female with recently implanted spermatophores was 94 mm CW. In this study, the observed smallest ovigerous female was 96 mm CW, which is similar to the smallest female with recently implanted spermatophores in the Queensland population.

Egg number and size are significantly correlated with female crab weight and carapace width. In the waters off northern Taiwan, gravid female *P. sanguinolentus* had from  $4.1 \times 10^5$  to  $2.44 \times 10^6$  eggs. The mode diameter was 270

$\mu\text{m}$ . These numbers were very similar to those for gravid female *P. sanguinolentus* in Indian waters, which had from  $9.6 \times 10^5$  to  $2.25 \times 10^6$  eggs (Ryan, 1967), and greater than estimates of  $4.4 \times 10^4$  to  $1.19 \times 10^6$  eggs for *P. sanguinolentus* in the waters off Karnataka, India (Sukumaran and Neelakantan, 1997). The discrepancy may be affected by environmental factors, including predation, parasitization, and temperature, which may affect the balance between the optimal number and size of eggs (Smith and Fretwell, 1974; Lawlor, 1976).

This study is the first on the growth, mortality, and reproduction of *P. sanguinolentus* in Taiwan. However, validation of growth estimates has not been undertaken because hard-parts are lost during molting. As noted, age determination is absolutely necessary for nearly all studies of population dynamics (Wolff and Soto, 1992; Marques *et al.*, 1994). Therefore, studies of the growth of cultivated crabs and tagged wild crabs are needed to develop and validate methods of age determination. In mortality analysis, biased estimates of growth parameters seriously affect estimates of population parameters, such as the instantaneous natural mortality rate (Lai and Gunderson, 1987; Lai *et al.*, 1996). Hence, more reliable estimates of natural mortality rate are still required. Further research is urgently needed on other population dynamics studies such as yield per recruit model and length-based models analyses for estimating crab recruitment and abundance.

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#### LITERATURE CITED

- Anonymous. 2000. Year-Books, 2000. Fisheries Administration, Council of Agriculture, Taipei, Taiwan.
- Bernard, D. R. 1981. Multivariate analysis as a means of comparing growth in fish.—*Canadian Journal of Fisheries and Aquatic Sciences* 38: 233–236.
- Bhattacharya, C. G. 1967. A simple method of resolution of a distribution into Gaussian components.—*Biometrics* 23: 115–135.
- Campbell, G. R., and D. R. Fielder. 1986. Size at sexual maturity and occurrence of ovigerous females in three species of commercially exploited portunid crabs in S.E. Queensland.—*Proceedings of the Royal Society Queensland* 97: 79–87.
- Chappag, B. R. 1957. On the marine crabs (Decapoda: Brachyura) of Bombay State.—*Journal of the Bombay Natural History Society* 54: 399–439.
- Cobb, J., and J. F. Caddy. 1989. The population biology of decapods. Pp. 327–374 in J. F. Caddy, ed. *Marine Invertebrate Fisheries: Their Assessment and Management*. Wiley Interscience, New York.
- Dai, A. Y., and S. L. Yang. 1991. *Crabs of the China Seas*. China Ocean Press, Beijing. 682 pp.
- Defeo, O., and R. S. Cardoso. 2002. Macroecology of population dynamics and life history traits of the mole crabs *Emerita brasiliensis* in Atlantic sandy beaches of South American.—*Marine Ecology: Progress Series* 239: 169–179.
- Gayaniilo, F. C. Jr., and D. E. Pauly. 1997. FAO-ICLARM Stock Assessment Tools (FiSAT): Reference Manual. FAO Computerized Information Series (Fisheries). 8, FAO, Rome. 262 pp.
- Gunderson, D. R. 1980. Using r-K selection theory to predict natural mortality.—*Canadian Journal of Fisheries and Aquatic Sciences* 37: 2266–2271.
- Hartnoll, R. G. 1982. Growth. Pp. 111–196 in D. E. Bliss, ed.-in-chief, *The Biology of Crustacea*. Vol. 2, L. G. Abele, ed., Embryology, Morphology, and Genetics. Academic Press, New York.
- Hsu, C. C., H. C. Chang, and H. C. Liu. 2000. Sex-variant morphometrics of the swimming crab, *Portunus sanguinolentus* (Herbst), from the waters off northern Taiwan.—*Journal of the Fisheries Society of Taiwan* 27: 175–185.
- Huang, R. F. 1993. Studies on the taxonomy and distribution of the portunid crabs (Crustacea: Decapoda: Brachyura) in Taiwan.—*Doctoral Dissertation*, National Taiwan Ocean University, Keelung, Taiwan. 235 pp. [In Chinese.]
- Jacob, R., P. N. Prasad, and M. S. Kusuma. 1990. Maturity and dimensional studies in female crabs of *Portunus sanguinolentus* and *P. pelagicus* (Decapoda: Portunidae).—*Indian Journal of Marine Sciences* 19: 221–223.
- King, M. 1995. *Fisheries Biology, Assessment and Management*. Fishing News Books, London. 341 pp.
- Lai, H. L., and D. R. Gunderson. 1987. Effects of ageing errors on estimates of growth, mortality and yield per recruit for walleye pollock (*Theragra chalcogramma*).—*Fisheries Research* 5: 287–302.
- , V. T. Gullucci, D. R. Gunderson, and R. F. Donnelly. 1996. Age determination in fisheries: methods and applications to stock assessment. Pp. 82–178 in V. F. Gullucci, S. B. Saila, D. J. Gustafson, and B. J. Rothschild, eds. *Stock Assessment, Quantitative Methods and Applications for Small-Scale Fisheries*. CRS, Lewis Publishers, New York.
- Lawlor, L. R. 1976. Parental investment and offspring fitness in the terrestrial isopod *Armadillidium vulgare* (Latr.) (Crustacea: Oniscoidea).—*Evolution* 30: 775–785.
- Leffler, C. W. 1972. Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory.—*Marine Biology* 14: 104–110.
- Marques, J. C., I. Martins, C. T. Ferreira, and S. Cruz. 1994. Population dynamics, life history, and production of *Cyathura carinata* (Kroyer) (Isopoda: Anthuridae) in the Mondego estuary, Portugal.—*Journal of Crustacean Biology* 14: 258–272.
- Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks.—*Journal du Conseil* 39: 175–192.
- , and J. L. Munro. 1984. Once more on the comparison of growth in fish and invertebrates.—*ICLARM Fishbyte* 2: 21.
- Quinn, T. J. II, and R. B. Deriso. 1999. *Quantitative Fish Dynamics*. Oxford, New York. 542 pp.
- Reeby, J., P. N. Prasad, and M. S. Kusuma. 1990. Size at maturity in male crabs of *Portunus sanguinolentus* and *P. pelagicus*.—*Fishery Technology* 27: 115–119.
- Ryan, E. P. 1967. Structure and function of the reproductive system of the crab, *Portunus sanguinolentus* (Herbst).—*Proceedings of the Symposium on Crustacea*, Marine Biology Association of India, Part II: 252–544.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring.—*American Naturalist* 108: 499–506.
- Stephenson, W., and B. Campbell. 1959. The Australian portunids (Crustacea: Portunidae). III. The genus *Portunus*.—*Australian Journal of Marine and Freshwater Research* 10: 84–124.
- Sukumaran, K. K., K. Y. Telang, and D. Thippeswamy. 1986. On the fishery and biology of the crab *Portunus sanguinolentus* (Herbst) along the south Kanara coast.—*Indian Journal of Fisheries* 33: 188–200.
- , and B. Neelakantan. 1997. Sex ratio, fecundity and reproductive potential in two marine portunid crabs, *Portunus (Portunus) sanguinolentus* (Herbst) and *Portunus (Portunus) pelagicus* (Linnaeus) along the Karnataka coast.—*Indian Journal of Marine Sciences* 26: 43–48.
- Sumpton, W. D., G. S. Smith, and M. A. Potter. 1989. Notes on the biology of the Portunid crab, *Portunus sanguinolentus* (Herbst), in subtropical Queensland waters.—*Australian Journal of Marine and Freshwater Research* 40: 711–717.
- Wenner, A. M. 1972. Sex ratio as a function of size in marine Crustacea.—*The American Naturalist* 106: 321–350.
- , D. M. Hubbard, J. Dugan, J. Shoffner, and K. Jellison. 1987. Egg production by sand crabs (*Emerita analoga*) as a function of size and year class (Decapoda, Hippidae).—*The Biological Bulletin* 172: 225–235.
- Wolff, M., and M. Soto. 1992. Population dynamics of *Cancer polyodon* in La Herradura Bay, northern Chile.—*Marine Ecology: Progress Series* 85: 69–81.
- Zar, J. H. 1995. *Biostatistical Analysis*. 3rd Edition. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.

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