CHALLENGES IN AQUATIC SCIENCES

Life history tactics of southern velvet shrimp *Metapenaeopsis palmensis* (Crustacea, Decapoda) in the waters off southwestern Taiwan

Hsu-Sen Chen · Chiee-Young Chen · Meng-Hsien Chen

Abstract The southern velvet shrimp, *Metapenaeopsis palmensis*, a small, tropical r-strategist shrimp, was investigated to test whether its life history tactics are similar to those of penaeid shrimps. In total, 7,832 shrimps were collected in southwestern Taiwan from April 2002 to August 2011. For the first time, we have identified the shrimp as a multiple spawner. This species has a size-segregated distribution, with the newly recruited early juveniles [<6.00 mm carapace length (CL)] living offshore (water depth = 30 m) and the subadults and mature spawning adults (CL ≥9.39 mm) living inshore (water depth = 15–20 m). They spawn from February to June before the rainy season when the water temperature exceeds 25°C. Only the larvae hatched in the late spawning season will successfully recruit in the dry season in September–November when the bottom water salinity is higher than 33.5 psu. The life history tactics of this species are different from those found by various previous studies on penaeid shrimps.

Keywords Multiple spawner · Optimal temperature for ovary development · Delay recruitment · Latitudinal effect · Salinity tolerance · Size-dependent bathymetric distribution

H.-S. Chen · M.-H. Chen
Department of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung 804, Taiwan

C.-Y. Chen (✉)
Department of Marine Environmental Engineering, National Kaohsiung Marine University, Kaohsiung 811, Taiwan
e-mail: chency@mail.nkmu.edu.tw

M.-H. Chen
Department of Oceanography, and Asia-Pacific Ocean Research Center, National Sun Yat-sen University, Kaohsiung 804, Taiwan

Introduction

Velvet shrimps, belonging to the genus *Metapenaeopsis*, contain the most numerous species (74 species) in the Penaeidae family, and are commercially and ecologically important (De Grave et al., 2009). They also play an important role in marine benthic food webs and serve as prey species to various benthic fishes (e.g., Linke et al., 2001; Raymundo-Huizar et al., 2005). However, the ecology of this genus is still unclear. Most studies have focused on certain commercially exploited species such as *M. barbata*, *M. dalei*, *M. palmensis*, and *M. rosea* in the Indo-West Pacific region (Hayashi & Sakamoto, 1978; Watson & Keating, 1989; Sakaji et al., 2000; Sakaji, 2003). The southern velvet shrimp, *M. palmensis*, is widely distributed in the coastal waters of the Indo-West Pacific region (Holthuis, 1980). Among 12 velvet

shrimp species found in the waters around Taiwan (Lee et al., 1999), this species is the most dominant, contributing more than 80% of the total catch of shrimp in the waters off the southwestern coast (Chen, 2006). It is also the most dominant among the three target species, *M. palmensis*, *M. barbata*, and *Trachysalambria curvirostris* of the local shrimp trawl fisheries in southwestern Taiwan.

The Kaoping River is a major river in southwestern Taiwan. This river yields an average sediment load of 11,000 T km^{-2} year^{-1}, ranking 12th in the world in terms of sediment load, and contributes almost half (15–35 million tons) of the total sediment load in this area (Milliman & Syvitski, 1992; Dadson et al., 2003; Liu et al., 2008). The average annual freshwater discharge of the river is 8.46 × 10^9 m^3, with 78% of discharge occurring between June and September (Chen et al., 2004). The large amount of sediment load and freshwater discharge of the river during the rainy/typhoon season leads to tremendous changes in salinity and turbidity in the coastal waters off southwestern Taiwan. In general, low salinity is thought to be an important factor attracting the larvae of estuary-dependent shrimp species such as *Penaeus* and *Metapenaeus* to migrate into lagoons or estuaries (Dall et al., 1990). However, the influence of salinity on this non-estuary-dependent species remains unknown.

To the best of our knowledge, previous studies on growth, reproduction, migration, and habitat usage have concentrated on the genera of *Penaeus* or *Metapenaeus*, the larger species of commercial value (e.g., Potter et al., 1989; Courtney et al., 1995). Only a few studies have investigated the biology and fisheries of *Metapenaeopsis* spp., in terms of their taxonomy (Hayashi & Sakamoto, 1978), spatiotemporal distribution, and reproductive biology in Japan and Australia (Hayashi & Sakamoto, 1978; Watson & Keating, 1989), among which none of the studies include information from Taiwan.

Therefore, the major goal of this study is to investigate the life history characteristics of *M. palmensis*, a tropical small r-strategist shrimp, and to elucidate how they cope with the seasonal fluctuations of the environment that they encounter, and the kind of life tactics which lead them to thrive as the dominant species in the study area. Moreover, such information is very important for the sustainable usage of the shrimp resource to support the livelihood of local fishermen.

Materials and methods

Study area and sample collection

The study area covers the major fishing grounds for shrimp trawl fisheries, and is located between the waters off Jiading and Fangliao in southwestern Taiwan (22°16′–22°54′N; 120°06′–120°32′E) (Fig. 1). Two sets of field data were used in this study. First, for the understanding of the seasonal variation of the *M. palmensis* population structure, shrimp samples were collected by Ocean Research vessel (R/V OR3) at seven stations, Jiading, Zuoying, Jhongjhou, Linyuan, Dapeng, Linbian and Fangliao, along the coast of southwestern Taiwan from April 2002 to August 2010. The samples were collected by a beam trawl, 6 m width and 8 m length and with a 40 mm stretched mesh at the body and 25 mm at the cod end, at depths ranging from 10 to 40 m. Each trawling was conducted for 30 min at 2 knots h^{-1} during the daytime (0600–1800), and all the samples were frozen below −20°C on board. Combining the overall shrimp catch data from April 2002 to August 2010, in total 31 cruises and 284 hauls of trawling data were used. The data were pooled monthly to yield at least one cruise and 15 hauls for each month. Environmental conditions, including surface and bottom water temperature, salinity and dissolved oxygen (DO), were recorded by an onboard conductivity–temperature–depth profiler (CTD). Second, fresh shrimp samples were collected monthly from the Kezailiao (KZL) fish market from January 2009 to August 2011 (Fig. 1) for the study of reproductive biology.

Sample treatment and preparation

In the laboratory, individuals were identified. All *M. palmensis* were sorted out and their gender was identified according to the presence (male) or absence (female) of petasma in the first abdominal legpleopod, and numbers were counted. The carapace length (CL) was measured to the nearest 0.01 mm, and body weight (BW) was weighed to 0.01 g. The ovary color inside the carapace was observed for the female shrimps collected from KZL fish market, and the

Fig. 1 Map showing the seven sampling sites (marked with *circles*), *JD* Jiading, *ZY* Zuoying, *JJ* Jhongjhou, *LY* Linyuan, *DP* Dapeng, *LB* Linbian, and *FL* Fangliao, collected by R/V OR3, and *Metapenaeopsis palmensis* purchased from a fishing port (marked with a *triangle*), *KZL* Kezailiao, in southwestern Taiwan
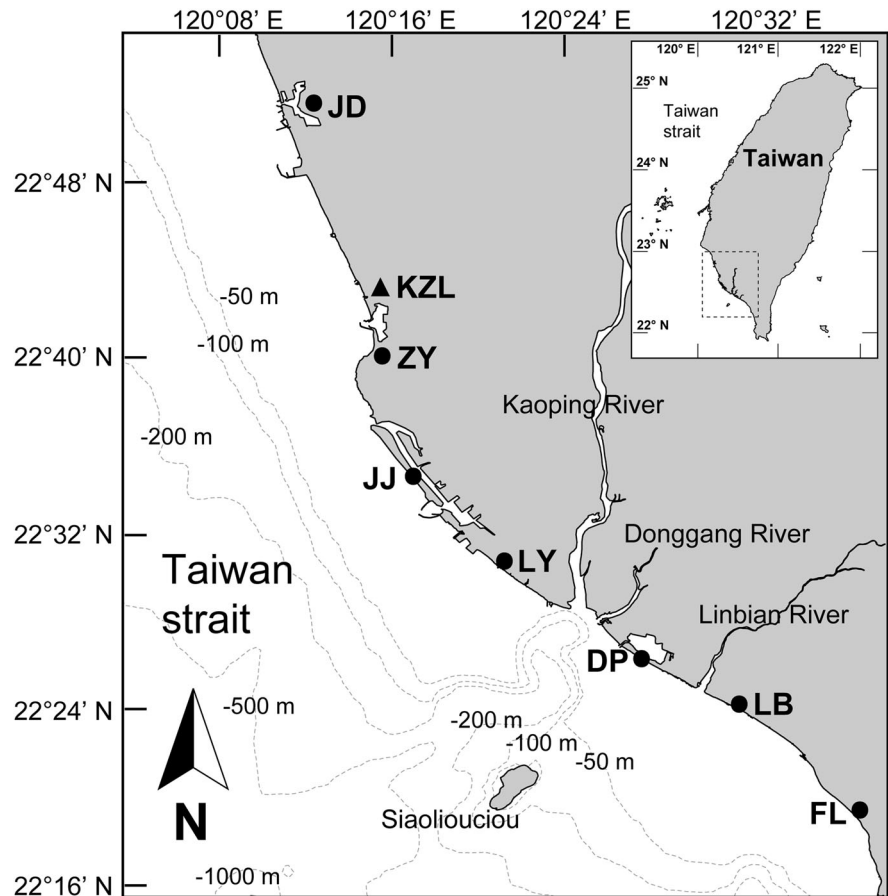

Table 1 Four ovary development stages are identified by the macroscopic characteristics, the histological characteristics, GSI, and the mean CL with range (min–max) for the female *M. palmensis*

Maturity	Macroscopic characteristics	Histological characteristics	GSI	CL (mm)
Immature	Ovary is thin and transparent in color	The oocytes development to stage I to stage II	0.85 ± 0.66 (0.05–2.56)	13.27 ± 2.25 (8.9–18.07)
Development	Ovary is turned to lightgreen in color, the anterior lobe is starting to development	The oocytes development to stage II to stage IV	3.00 ± 1.40 (0.30–6.58)	15.53 ± 2.94 (12.18–18.94)
Premature	Ovary is green in color, the anterior lobe, medium lobe, and posterior lobe are full development	The oocytes are development to stage II to stage V	3.51 ± 1.17 (0.7–6.17)	15.63 ± 3.43 (12.16–19.61)
Mature	Ovary is darkgreen in color, the mature eggs are visible by the naked eyes	The oocytes are development to stage II to stage VI	4.28 ± 1.24 (1.74–7.05)	14.83 ± 4.08 (9.39–20.24)

gonadal development stages were identified by sight according to the characteristics established according to the histological results of the ovarian section and macroscopic view in this study stated in a later section (Table 1, Yano, 1988; Sakaji, 2001). The gonad of the female shrimp was dissected out and weighed to gain

the gonad weight (GW), then fixed in 10% neutral-buffered formalin for further histological examination.

The formalin-fixed ovarian tissue of each shrimp was dehydrated in ethanol, embedded in paraffin, sectioned to 5–7 μm, and stained by hematoxylin–eosin (H&E). The oocyte development stages were
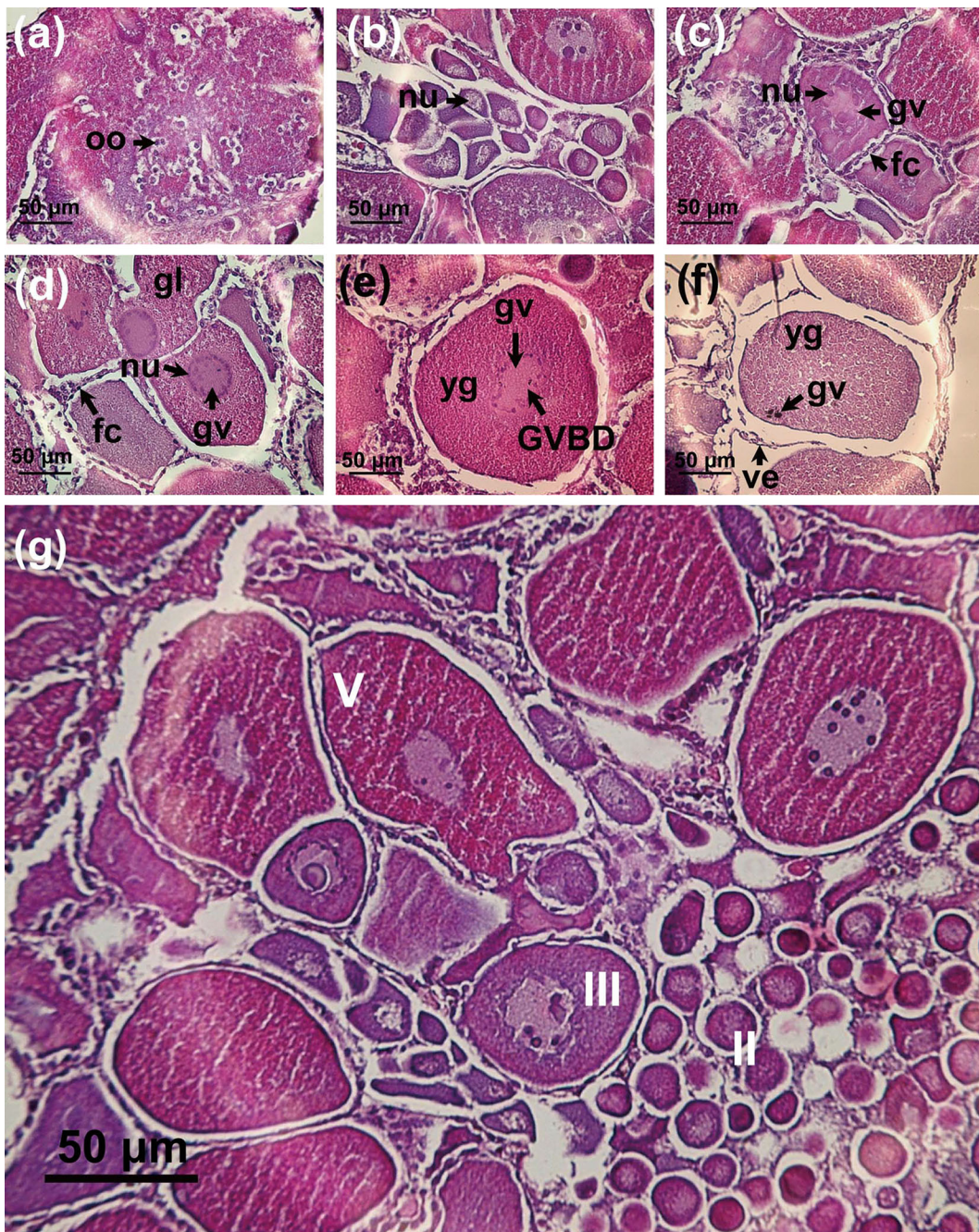
Fig. 2 Histological sections of developmental oocyte and mature gonad of *M. palmensis*. Sections were stained by hematoxylin–eosin (H&E) stain. **a–f** Oocyte development stage, *scale bar* 50 μm. **g** Histological section of mature gonad with various oocytes, *scale bar* 100 μm (CL = 17.83 mm; GSI = 3.69). *oo* oocyte, *nu* nucleoli, *gv* germinal vesicle, *GVBD* germinal vesicle break down, *fc* follicle cell, *gl* globule, *ve* vitelline envelope, *yg* yolk granule

determined according to the criteria of Yano (1988) and Sakaji (2001). Six oocyte development stages of *M. palmensis* can be distinguished, according to size, nucleolus, and germinal vesicle location (Fig. 2). The characteristics of each stage were identified as follows:

Stage I   Oocytes are round, basophilic and of the same size (ca. 10 μm in diameter) situated in the connective tissue of the ovary (Fig. 2a).

Stage II   The oocytes are 20–50 μm in diameter. A strongly basophilic chromatin is found in the nucleus, and the cytoplasm is weakly basophilic (Fig. 2b).

Stage III   The oocytes are 70–120 μm in diameter, and covered with a thick layer of well-developed follicle cells. The nucleoli are visible and are distributed along the margin of the germinal vesicle (Fig. 2c).

Stage IV   The oocytes are 150–180 μm in diameter. Circular nucleoli lie peripherally in the germinal vesicle. A number of globules are found in the basophilic cytoplasm. The layer of follicle cells becomes thinner than at stage III (Fig. 2d).

Stage V   The oocytes are 150–200 μm in diameter. The germinal vesicle breakdown (GVBD) can be observed in this stage. Acidophilic yolk granules stained by Eosin are found in the cytoplasm (Fig. 2e).

Stage VI   The oocytes are 200–250 μm in diameter. The germinal vesicle is shrunk and shifts to the edge of the oocyte. The acidophilic yolk granules are concentrated and fill the cytoplasm of the oocyte (Fig. 2f).

The histological results of ovary sections were integrated with the macroscopic observation, then the arbitrary observation of ovary development can be distinguished as four stages: (1) immature (Stage I), (2) development (Stage D), (3) premature (Stage P), and (4) mature (Stage M) for female *M. palmensis* ovaries (Table 1).

Statistics

The gonadosomatic index (GSI) was calculated as

$$GSI = GW/(BW - GW) \times 100. \qquad (1)$$

The CL at 50% maturity for both males and females can be calculated by the following equation:

$$P = 1/1 + \exp(a + b \times CL), \qquad (2)$$

with the logarithmic transformation given by Eq. (3):

$$\ln[(1 - P/P)] = (a + b\ CL), \qquad (3)$$

where P is the predicted mature proportion, a and b are the estimated coefficients of the logistic equation, and CL is the carapace length (in mm). The estimation of the parameters in this equation is made by correlation analysis of the variables P and CL after linearization by the residual-squared sum model. Size at sexual maturity (CL50) corresponds to a proportion of 0.5 sexually mature individuals. When the estimate is a negative value, the ratio of the coefficients [CL50 $= -(a/b)$] is then substituted by $P = 0.5$ in Eq. (2).

Results

Environmental factors

Significant seasonal variations in temperature, salinity, DO, and precipitation were found (Table 2) from monthly environmental variables (mean ± SD) recorded during the OR3 sampling period from April 2002 to August 2010, as well as the monthly precipitation data obtained from the Central Weather Bureau (http://www.cwb.gov.tw) from 2002 to 2010 (Table 2). The lowest sea bottom temperature occurred in December (24.03 ± 0.44°C), whereas the highest occurred in July (29.74 ± 0.66°C). In contrast, the salinities of the study area showed different patterns. The lowest salinity was found in August (32.92 ± 0.46 psu), and the highest in January (34.45 ± 0.15 psu). The DO concentrations were all higher than 4.0 ppm throughout the study period. It is clear that there was no hypoxia [DO <2.0 ppm (Diaz, 2001)] found in the study area at any time. The rainy season is from May to September, and is identified by a monthly average precipitation of more than 100 mm. The highest average precipitation occurred in June (508.6 ± 67.7 mm).

Monthly GSI variation of the shrimp collected from KZL fishing port

The shrimp collected from KZL fish market were grouped into three groups by CL (in mm), namely, small = 8.01 ≤ CL < 12.00 mm, medium = 12.00 ≤ CL < 17.00 mm, and large = 17.00 ≤ CL < 22.00 mm. Then, the monthly GSI variations were presented by the size groups, showing a similar pattern among the three groups. However, the monthly variation of GSI of the small group had a slightly

Table 2 The monthly environmental variables (mean ± SD) recorded in 31 cruises of OR3 surveys from April 2002 to August 2010 in waters off southwestern Taiwan

	January	February	March	April	May	June
Surface temperature (°C)						
Day	24.06 ± 0.71	24.64 ± 0.92	24.95 ± 0.49	26.34 ± 0.59	27.74 ± 0.50	29.33 ± 0.66
	(21.90–25.55)	(23.71–25.95)	(23.94–25.88)	(25.31–27.27)	(26.47–28.51)	(28.17–30.16)
Night	23.28 ± 0.79	24.39 ± 0.89	25.68 ± 0.16	26.83 ± 0.78	–	28.17 ± 0.06
	(22.05–24.08)	(23.66–25.86)	(25.49–25.78)	(25.60–27.82)		(28.11–28.22)
Bottom temperature (°C)						
Day	23.61 ± 0.52	24.34 ± 1.08	24.50 ± 0.53	24.89 ± 0.85	25.72 ± 1.00	27.25 ± 1.35
	(21.89–24.43)	(22.60–25.91)	(22.93–25.40)	(22.56–25.86)	(23.06–27.40)	(22.77–29.13)
Night	23.12 ± 0.84	24.18 ± 0.85	24.65 ± 0.18	26.45 ± 0.62	–	27.43 ± 0.29
	(21.90–23.95)	(23.51–25.67)	(24.51–24.85)	(25.48–27.05)		(27.18–27.74)
Surface salinity (psu)						
Day	34.32 ± 0.26	34.33 ± 0.10	34.51 ± 0.10	33.92 ± 0.04	34.36 ± 0.17	33.53 ± 0.30
	(33.66–34.65)	(34.18–34.45)	(34.21–34.69)	(33.85–34.02)	(33.89–34.62)	(32.84–33.94)
Night	34.45 ± 0.24	34.29 ± 0.22	34.40 ± 0.06	33.94 ± 0.20	–	33.26 ± 0.36
	(34.12–34.74)	(33.94–34.45)	(34.33–34.45)	(33.74–34.29)		(32.84–33.50)
Bottom salinity (psu)						
Day	34.45 ± 0.15	34.38 ± 0.14	34.55 ± 0.10	34.06 ± 0.09	34.54 ± 0.16	34.05 ± 0.24
	(34.26–34.67)	(34.18–34.57)	(34.27–34.71)	(33.91–34.25)	(34.30–34.99)	(33.74–34.80)
Night	34.54 ± 0.18	34.38 ± 0.13	34.49 ± 0.03	34.06 ± 0.29	–	33.87 ± 0.12
	(34.30–34.72)	(34.21–34.51)	(34.46–34.52)	(33.82–34.54)		(33.74–33.96)
Surface D.O. (ppm)						
Day	4.82 ± 0.06	4.77 ± 0.07	4.74 ± 0.04	4.65 ± 0.05	4.53 ± 0.04	4.44 ± 0.05
	(4.71–5.00)	(4.67–4.85)	(4.67–4.83)	(4.58–4.73)	(4.47–4.63)	(4.38–4.53)
Night	4.89 ± 0.06	4.80 ± 0.07	4.69 ± 0.01	4.61 ± 0.06	–	4.53 ± 0.01
	(4.82–4.99)	(4.68–4.87)	(4.68–4.70)	(4.54–4.70)		(4.52–4.53)
Bottom D. O. (ppm)						
Day	4.86 ± 0.04	4.80 ± 0.09	4.78 ± 0.04	4.76 ± 0.07	4.68 ± 0.08	4.58 ± 0.10
	(4.78–5.00)	(4.67–4.94)	(4.70–4.91)	(4.69–4.95)	(4.55–4.90)	(4.44–4.93)
Night	4.90 ± 0.07	4.81 ± 0.07	4.77 ± 0.02	4.64 ± 0.04	–	4.57 ± 0.02
	(4.83–5.00)	(4.69–4.87)	(4.75–4.78)	(4.60–4.70)		(4.55–4.58)
Precipitation (mm)[a]	12.2 ± 2.7	12.3 ± 2.4	17.2 ± 5.1	48.5 ± 8.5	156.5 ± 30.8	508.6 ± 67.7
	(9.8–15.1)	(10.5–15.0)	(12.0–22.1)	(41.9–58.2)	(123.0–183.7)	(456.4–585.1)

	July	August	September	October	November	December
Surface temperature (°C)						
Day	29.74 ± 0.66	29.68 ± 0.51	28.72 ± 0.83	27.93 ± 0.32	26.16 ± 0.57	24.03 ± 0.44
	(28.83–31.74)	(29.01–30.78)	(25.30–29.80)	(27.37–28.47)	(24.85–27.12)	(23.41–24.43)
Night	29.51 ± 0.29	–	29.21 ± 0.07	28.84 ± 0.77	–	23.79 ± 0.64
	(28.92–29.78)		(29.16–29.26)	(27.72–29.96)		(22.56–24.36)
Bottom temperature (°C)						
Day	28.61 ± 1.02	28.30 ± 0.79	27.89 ± 1.07	27.54 ± 0.24	25.62 ± 0.73	23.52 ± 0.68
	(25.74–29.82)	(27.08–29.47)	(23.74–29.15)	(26.97–27.91)	(23.91–26.84)	(22.83–24.14)
Night	28.14 ± 0.40	–	28.66 ± 0.21	28.10 ± 0.47	–	23.54 ± 0.48
	(27.49–28.66)		(28.51–28.81)	(27.24–28.71)		(22.82–24.14)

Table 2 continued

	July	August	September	October	November	December
Surface salinity (psu)						
Day	33.44 ± 0.56	32.92 ± 0.46	33.02 ± 0.97	33.81 ± 0.11	34.25 ± 0.19	34.47 ± 0.10
	(31.86–34.07)	(31.80–33.50)	(29.57–34.74)	(33.50–33.92)	(33.76–34.50)	(34.32–34.54)
Night	33.14 ± 0.77	–	32.97 ± 0.37	33.34 ± 0.58	–	34.35 ± 0.14
	(32.24–34.03)		(32.71–33.23)	(32.25–34.02)		(34.16–34.53)
Bottom salinity (psu)						
Day	33.80 ± 0.26	33.57 ± 0.17	33.82 ± 0.38	34.00 ± 0.09	34.38 ± 0.19	34.42 ± 0.10
	(33.29–34.12)	(33.28–33.78)	(33.11–34.36)	(33.86–34.17)	(33.77–34.65)	(34.32–34.52)
Night	33.87 ± 0.17	–	33.78 ± 0.25	33.94 ± 0.09	–	34.44 ± 0.08
	(33.65–34.05)		(33.61–33.96)	(33.77–34.06)		(34.30–34.50)
Surface D.O. (ppm)						
Day	4.41 ± 0.05	4.43 ± 0.04	4.49 ± 0.06	4.53 ± 0.02	4.65 ± 0.04	4.82 ± 0.04
	(4.27–4.47)	(4.34–4.47)	(4.43–4.73)	(4.49–4.57)	(4.58–4.75)	(4.78–4.88)
Night	4.43 ± 0.02	–	4.46 ± 0.01	4.48 ± 0.04	–	4.84 ± 0.06
	(4.40–4.47)		(4.45–4.47)	(4.42–4.54)		(4.79–4.95)
Bottom D. O. (ppm)						
Day	4.48 ± 0.07	4.51 ± 0.06	4.53 ± 0.08	4.55 ± 0.02	4.69 ± 0.06	4.87 ± 0.06
	(4.39–4.69)	(4.43–4.60)	(4.46–4.85)	(4.53–4.60)	(4.60–4.83)	(4.81–4.93)
Night	4.51 ± 0.03	–	4.48 ± 0.01	4.51 ± 0.03	–	4.86 ± 0.04
	(4.47–4.56)		(4.47–4.48)	(4.47–4.58)		(4.81–4.93)
Precipitation (mm)[a]	450.0 ± 100.4	444.6 ± 74.4	281.9 ± 107.0	58.3 ± 17.7	26.9 ± 5.3	25.8 ± 6.5
	(388.3–565.8)	(376.4–524.0)	(185.0–396.7)	(43.7–78.1)	(22.2–32.6)	(21.0–33.2)

[a] Data collected by Central Weather Bureau at Tainan, Kaohsiung and Pingtung from 2002 to 2010

Fig. 3 Monthly variation of GSI and sample size of female *M. palmensis* for three CL groups. All samples were collected from Kezailiao fish market from January 2009 to August 2011 in the waters off southwestern Taiwan
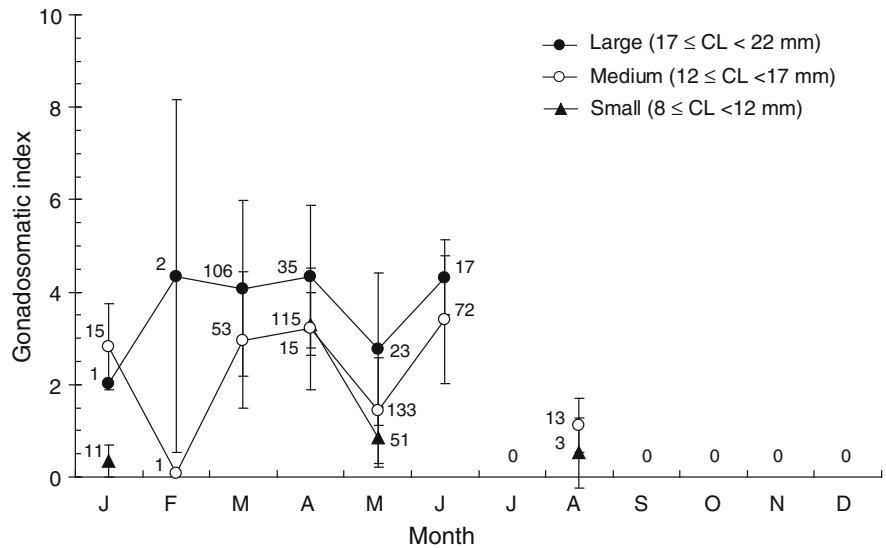
lower value than the medium and large groups throughout the study period, except for April. The monthly variation of GSI of the medium and large groups raised in February and peaked in April, with a drop in May and then another rise in June. No large individuals could be collected after July and no shrimp

Table 3 The percentage of various female gonad development stages for gonadosomatic indices of *M. palmensis* in the waters off southwestern Taiwan

GSI range	Gonadal development stage				
	Immature (%)	Development (%)	Premature (%)	Mature (%)	Number (%)
0–1	80	18	2	0	44
1–2	23	43	21	13	56
2–3	3	32	57	8	60
3–4	0	27	50	23	60
4–5	0	34	47	19	58
5–6	0	18	36	46	28
6–7	0	20	30	50	10
≥ 7	0	0	0	100	2

catches could be obtained from the fish market after August (Fig. 3).

In the histological sections, no postovulated oocytes were found. Ovaries containing Stage IV oocytes are the characteristic of gonadal maturation. Various oocyte developmental stages were found in the mature ovaries, indicating that the oocyte developmental pattern of *M. palmensis* is asynchronous and capable of spawning several times in one reproductive season.

Size at sexual maturity

As a whole, females with GSI <1 constituted 80% of the immature shrimps. Females with GSI >2 contained immature and mature shrimps, and constituted more than 50% of the premature and mature shrimps. Therefore, GSI ≥ 2 was used as an index of ovary maturity for *M. palmensis* (Table 3) for the further estimation of 50% maturation. The minimum and 50% maturity size of female *M. palmensis* were then estimated to be 9.39 and 12.72 mm, respectively (Fig. 4). Accordingly, four growth stages based on carapace length (mm) are defined for further elucidation of the relationship between shrimp maturity and environment: (1) Early juveniles are the shrimps with CL ≤ 6.00 mm, (2) Juveniles are CL = 6.01–9.38 mm, (3) Subadults are CL = 9.39–12.71 mm, and (4) Adults are CL ≥ 12.72 mm.

Size-frequency distribution

The occurrence of *M. palmensis* showed a seasonal variation with a single mode recruitment pattern in southwestern Taiwan from the data collected by the
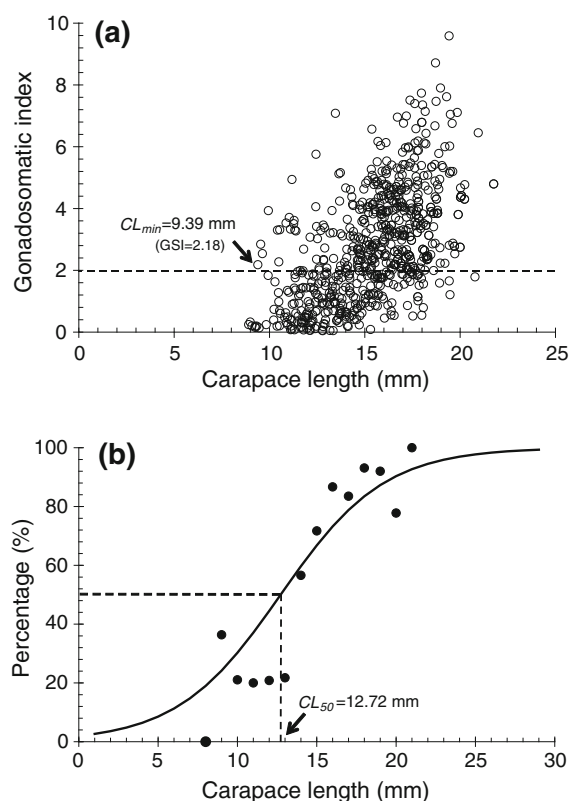
Fig. 4 Graph showing **a** the minimum CL of maturity (CLmin) of female *M. palmensis*. The *dash line* indicates GSI = 2. **b** The estimated first CL of maturity of female *M. palmensis* under GSI = 2

OR3 trawling survey from April 2002 to November 2003 (Fig. 4). The maximum CLs were 22.20 mm for males and 26.61 mm for females. The highest abundance of individuals occurred between March and June, with a peak mode in length frequency between 12.01 and 13.00 mm. However, a smaller peak mode
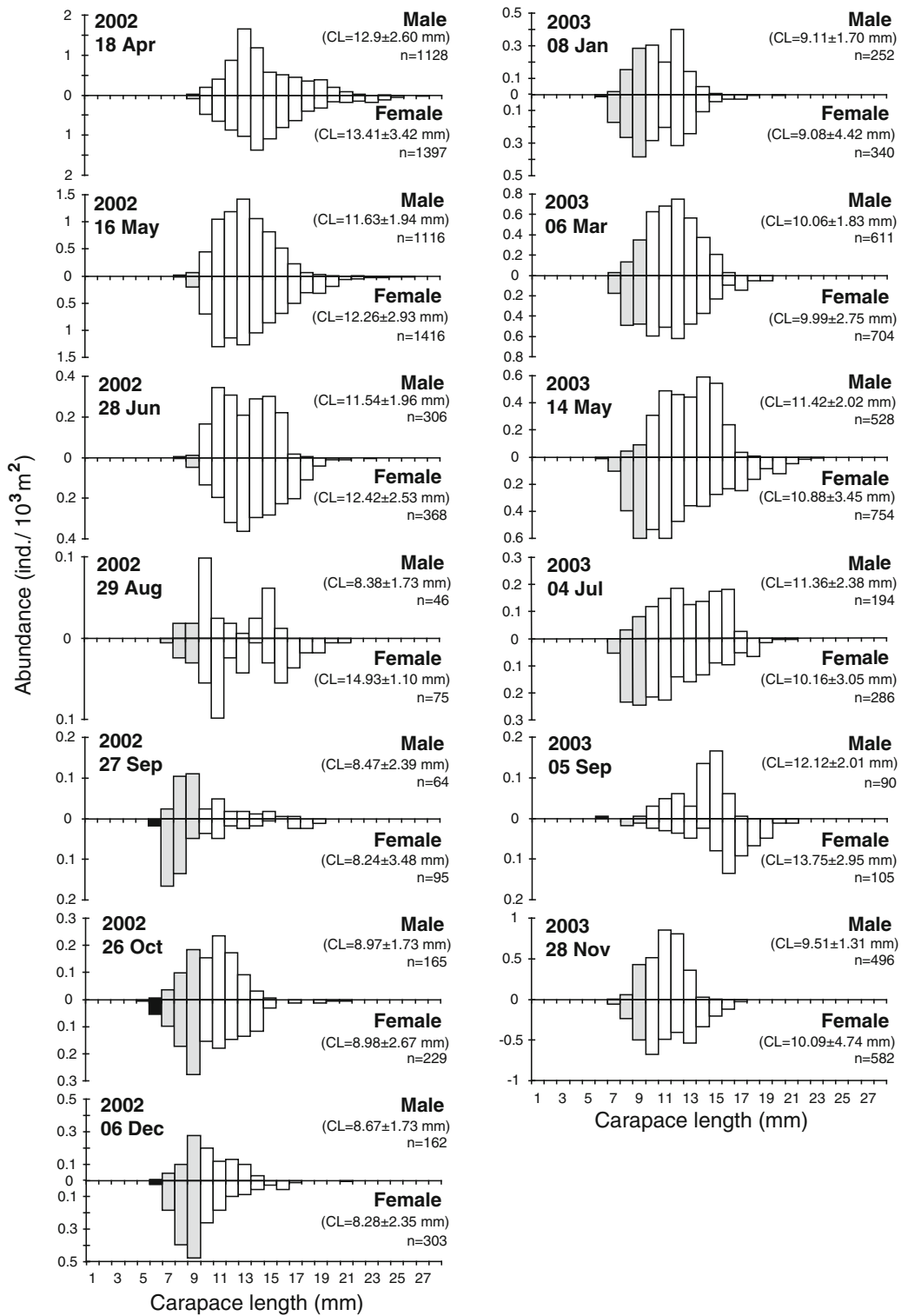
Fig. 5 Frequency distribution of CL for both sexes of *M. palmensis* collected from April 2002 to November 2003, collected by R/V OR3 in the waters off southwestern Taiwan.

White and *gray bars* indicate the size groups with CL ≥9.00 mm and CL = 6.01–8.99 mm, respectively, whereas the *black bar* indicates the group with CL ≤6.00 mm
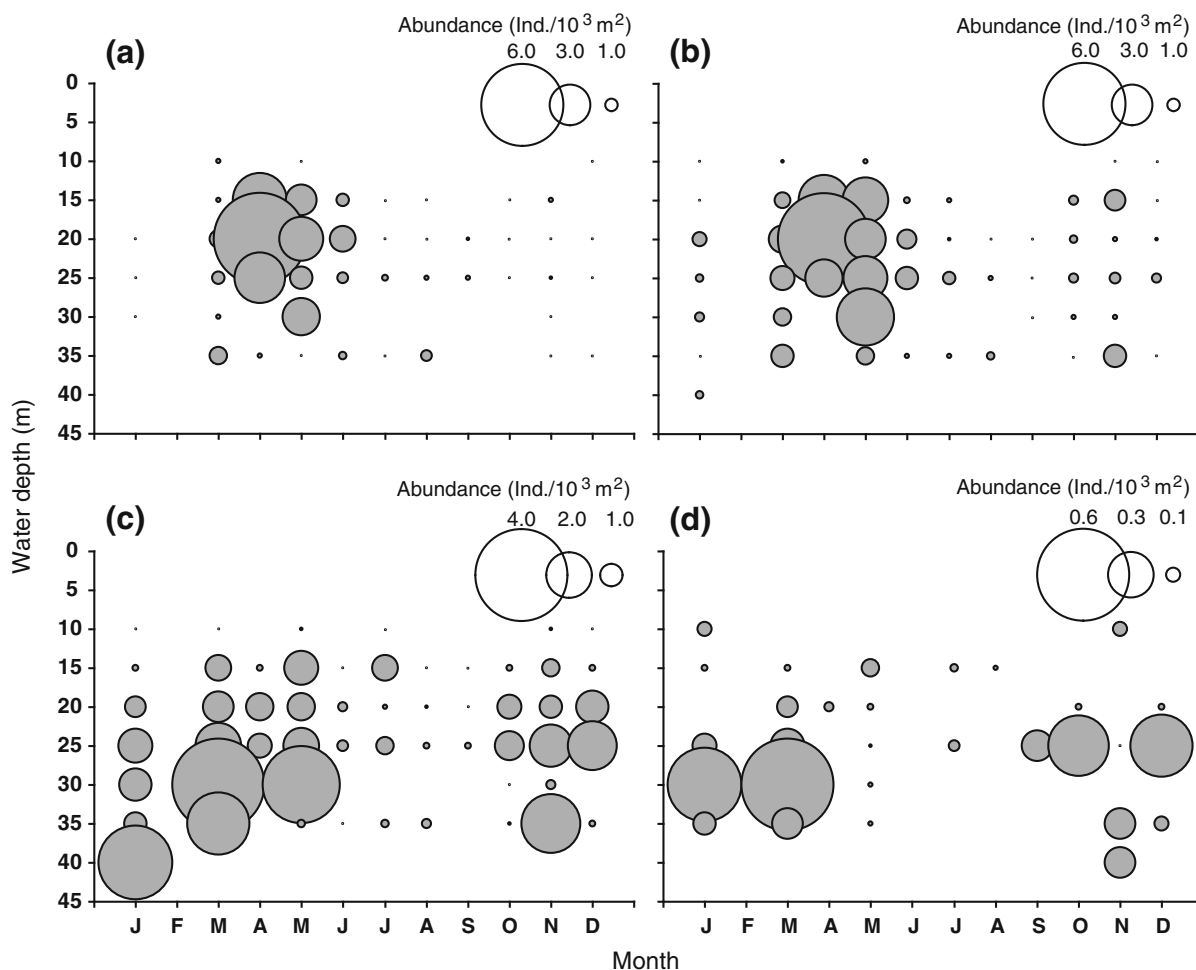
Fig. 6 The monthly abundance along with water depth for the four different growth stages, **a** adult (CL $\geqq$ 12.72 mm), **b** subadult (9.39 mm $\leqq$ CL < 12.72 mm), **c** juvenile (6.00 mm $\leqq$ CL < 9.39 mm), and **d** early juvenile (CL <6.00 mm), plotted by *bubble graph*

size was found during late July to September, while newly settled early juveniles (CL ≤6.00 mm) were found from September to December (Fig. 5).

Spatiotemporal distribution pattern of adults and juveniles

Adult and juvenile *M. palmensis* exhibit different spatiotemporal distribution patterns which are positively related with the increase in salinity. The abundance of adults and subadults starts to increase in February and peaks between April and May at depths of 15–25 m (2.30–6.63 ind./1000 m²). In the period from July to September, the abundance of each developmental stage of the shrimp decreases with very few individuals occurring (Fig. 6). In September,

recruitment of the current year's early juveniles and juveniles occurs at depths of 25–35 m. Few early juvenile or juvenile individuals could be observed at a depth of less than 20 m. Integrating the spatiotemporal distribution pattern and monthly GSI variation, we conclude that the adults (CL >13 mm) aggregate to spawn at a depth ranging from 15 to 25 m in February–June and their juveniles of the current year recruit in depths of between 25 and 35 m (Fig. 6).

Environment and recruitment patterns

The abundance of different growth stages of *M. palmensis* shows a significant seasonal pattern in relation to precipitation, water level, and salinity (Fig. 7). The highest abundance of the total catch
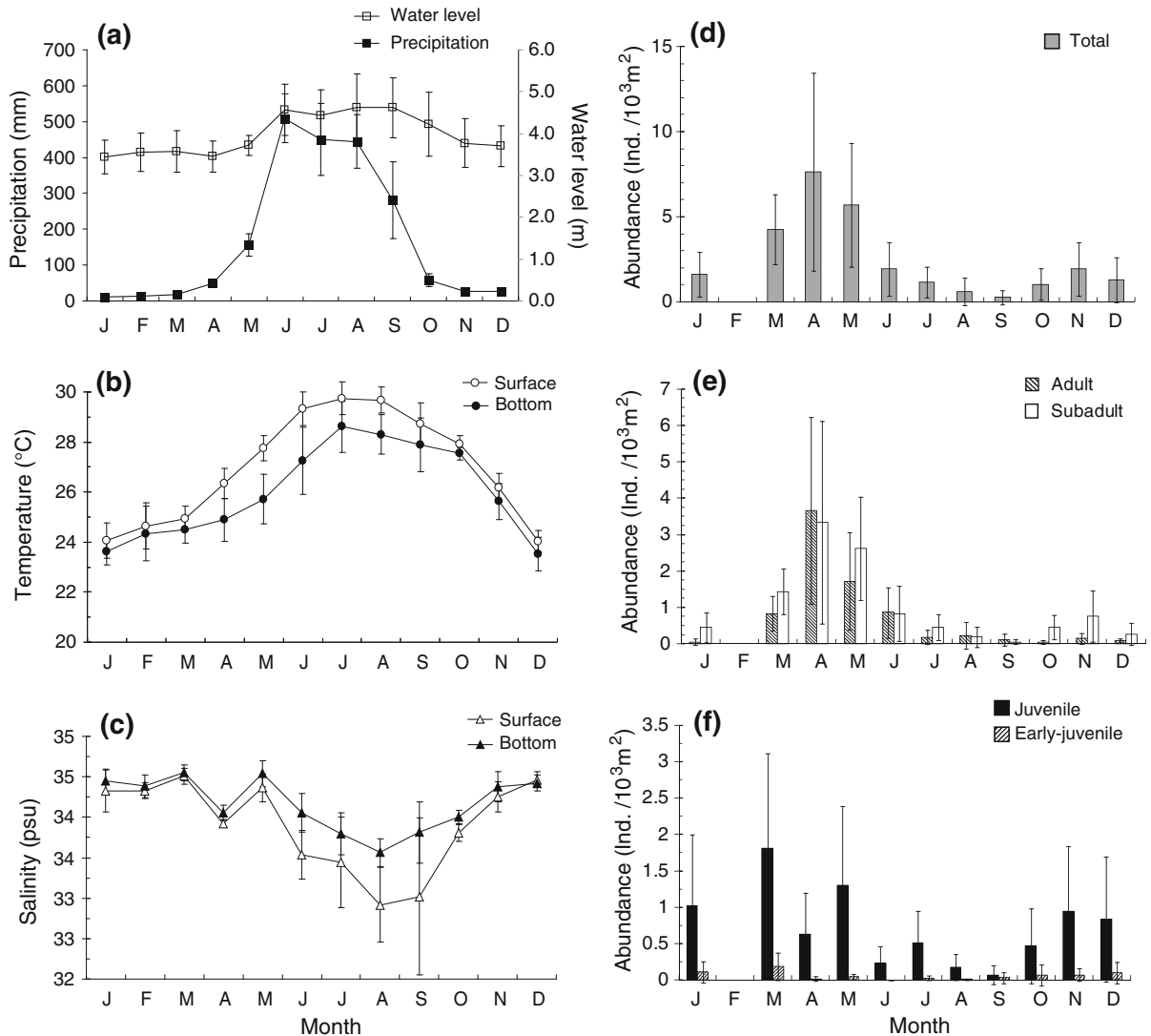
Fig. 7 The monthly **a** precipitation and water level, **b** surface and bottom water temperature, and **c** surface and bottom salinity recorded at the study area compared with the abundance of

d total female specimens, **e** adults and subadults, and **f** juveniles and early juveniles of *M. palmensis* in the waters off southwestern Taiwan

occurs in April and May before the rainy season from June to August (Fig. 7a, d). Fewer adults, subadults, and juveniles were collected between May and September when salinity dropped during the rainy season (Fig. 7c). Early juveniles appear in higher abundances from September to the following January after the rainy season (Fig. 7f).

According to the Pearson's correlation coefficient comparing the four growth stages and the environmental factors, the abundance of juveniles and early

juveniles showed a significantly negative correlation with the surface temperature and precipitation, as it did for the juveniles and bottom temperature. However, the abundance of subadults, juveniles, and early juveniles showed a significantly positive correlation with surface salinity, as it did with the juveniles and early juveniles with bottom salinity (Table 4). Therefore, the success of the recruitment of juvenile *M. palmensis* was in close conjunction with various environmental factors; in particular, salinity would be a controlling factor.

Table 4 The Pearson's correlation coefficient and the significant level between environmental factors and different growth phases of female *M. palmensis* in the waters off southwestern Taiwan

	Adult	Subadult	Juvenile	Early juvenile	Total
Temperature (°C)					
Surface	−0.12	−0.23	−0.52**	−0.37*	−0.32
Bottom	−0.18	−0.30	−0.51**	−0.32	−0.38*
Salinity (psu)					
Surface	0.06	0.38*	0.68***	0.41*	0.41*
Bottom	0.08	0.28	0.66***	0.40*	0.37*
Precipitation (mm)	0.06	−0.21	−0.44*	−0.42*	−0.21

* $\alpha = 0.05$; ** $\alpha = 0.01$; *** $\alpha = 0.001$

Discussion

Reproductive biology

Metapenaeopsis reveals a different oocyte development characteristic compared to other penaeid shrimps. They have a characteristic of GVBD (Yano, 1995; Sakaji et al., 2000; Sakaji, 2001) instead of the occurrence of cortical crypts (=cortical rods) (Clark et al., 1980; Ohtomi & Matsuoka, 1998; Kruevaisayawan et al., 2010; Villalobos-Rojas & Wehrtmann, 2011) as the characteristic for oocyte maturation. They have asynchronized development of oocytes identifying them as a multiple spawning shrimp species (Yamada et al., 2007; Hossain & Ohtomi, 2008).

Sea water temperature controls the reproduction of *Metapenaeopsis* shrimps. That is similar to the spawning of other penaeid shrimps stimulated by temperature shock (Yano, 1995). Although no optimal temperature for reproduction of *M. palmensis* has been established, previous studies of penaeid shrimps have indicated that the suitable water temperature for their gonad maturation and spawning is above 25°C in tropical/subtropical waters (e.g., Hoang et al., 2002; Aktaş et al., 2003). Their gonad development and spawning might cease when the temperature drops below 25°C in late summer and autumn (Crocos & Kerr, 1986; Robertson et al., 1991 in Aktaş et al., 2003). The same phenomenon was found for *M. palmensis* in southwestern Taiwan. Our in situ measured bottom water temperature in the spawning season (February–June) was 22.6–29.13°C and there was a rise to 25°C in February, and then would trigger the development of the ovary. It is similar to the spawning temperature for *P. semisulcatus* at 24–28°C

in Turkey (Kumlu et al., 1999). The rise in temperature not only triggers the gonad development of *M. palmensis*, but may also be associated with the cycle and success of the molting stage (Yamada et al., 2007; Kumlu et al., 2011), as well as limiting the northern boundary of their geographical distribution (Sakamoto & Hayashi, 1977).

Population dynamics and latitudinal analysis

The decrease in the duration of *M. palmesis*'s reproduction and the delay in the onset of its spawning correspond to the increase in latitude and the temperature. In tropical waters (9°30′S–10°10′S), their reproductive season could last throughout the year (Watson & Keating, 1989), but it is relatively shorter (June–September) in higher latitude waters (35°20′N–35°30′N) (Hayashi & Sakamoto, 1978). The spawning of *M. palmensis* in southwestern Taiwan (22°15′N–22°45′N) lasts for close to half a year from February to June, which falls between these two previous studies and corresponds to their latitudinal belongings that provide the optimal temperature for their survival and spawning. This shows that their intermediary location allows them to spawn for 5 months while the temperature is rising within an adequate range. Such a result adds one more example of shrimp having a gradual decrease in duration of reproduction and a delay in their spawning month as the latitude increases, as was found in the Gulf of California (Aragón-Noriega & Alcántara-Razo, 2005).

The latitudinal effect not only influences the duration and onset of shrimp spawning, but also the spawning frequency of *M. palmensis*. Its short-spawning period in the northern area reveals that

individual female shrimps spawn only once in a spawning season, as found in Japan (Hayashi & Sakamoto, 1978). In contrast, in the tropical area, there is a long period of optimal spawning temperature which allows the female shrimp to spawn more than once and throughout the year, as previously found in Australia (Watson & Keating, 1989). Such a phenomenon was also found by Aragón-Noriega & Alcántara-Razo (2005) who studied the brown shrimp, *Farfantepenaeus californiensis*, in the Gulf of California. Our findings for *M. palmensis* follow the trend of these previous studies.

Recruitment and distribution versus environmental parameters

Salinity plays an important role in the recruitment of *M. palmensis*. As with penaeid shrimps, salinity is an important factor contributing to high stocks in the rainy season (Dall et al., 1990; Gammelsrød, 1992). In this study, fewer juveniles and early juveniles settled at any depths during the rainy season, showing that the low salinity and high precipitation had negative effects. This indicated that *M. palmensis* juveniles seem less tolerant to low salinity. Although the mechanisms of how the salinity and precipitation act on juvenile recruitment are still unclear, Lin et al. (1992) found that turbidity would reduce the osmoregulatory capacity of late juvenile shrimps. The Kaoping River carries a large amount of freshwater and terrestrial sediments into our study area in the rainy season, not only reducing the salinity but also raising the turbidity (Chen et al., 2004; Liu et al., 2009). This affects the survival of the shrimp larvae, leading them to successfully recruit after the rainy season, showing a time lag between the reproductive season and the recruitment of early juveniles.

The size-dependent bathymetric distribution of *M. palmensis* also reveals a high restriction of temperature and salinity. In this study, an inshore spawning migration for adults could be observed. The juveniles tend to inhabit offshore waters at 25–35 m, and then they migrate to inshore waters at 15–25 m when they reach sexual maturity in spring, thus also avoiding resource competition (Pechenik, 1999). This phenomenon is in contrast to the life cycle of most penaeid shrimp whose juveniles inhabit shallow water and then migrate offshore for spawning (Dall et al., 1990). The more stable conditions in the dry season give them a

better chance of survival by settling in the offshore waters. Their life history characteristics of small size, short lifespan, and multiple spawning suggest that they are typical r-strategists with a high population recovery rate making a quick population recovery in highly disturbed waters (Pianka, 1970).

The recruitment of *M. palmensis* is delayed at least half a year from their first spawning action due to inadequate environmental conditions. The recruitment of penaeid juveniles is highly dependent on environmental factors (Dall et al., 1990). In our study, *M. palmensis* were found to spawn from February to June, and so their juveniles should recruit 3–4 months after hatching according to the CL-frequency distribution (by 1 mm intervals) estimated using FiSAT ELEFAN (H. S. Chen, unpublished data). However, they were first found to recruit in September to November, suggesting that the early born larvae did not recruit in the rainy season before September. Such a delayed recruitment phenomenon was also found for *Trachsalambria curvirostris* in central and southern Tokyo Bay, due to a hypoxia in spring to autumn (Yamada et al., 2007), and the juveniles of the *Metapenaeopsis* species in the western Atlantic Ocean region (Criales et al., 2000). In our case, only those *M. palmensis* larvae which spawned 3–4 months before the end of the rainy season could recruit successfully. The early juveniles can settle to the bottom in response to the increased salinity at the end of the rainy season, and the large amount of terrestrial detritus deposited in the rainy season became their major food source (Riera et al., 2000). Therefore, only one recruitment from the late reproductive season stock (May–June) is successful, while the early reproductive season stock (February–April) fail to settle during the rainy season. Such a delayed recruitment and offshore recruitment phenomenon reflects that they are stenohaline shrimp which need high salinity to survive.

Our findings provide very important information for fisheries management and policy making regarding the sustainable usage of this shrimp resource. For example, (1) according to the result of its spawning season and successful recruitment time, we can set an allowable fishing period from February to April which would enable the late spawning larvae to settle and recruit for the next year's population, and (2) according to the 50% maturity of females and males with a CL of 9.39 and 12.72 mm, respectively, we can set the cod end mesh size to not smaller than 4 cm to avoid

catching the first mature shrimp, thus leaving the smallest mature shrimp to spawn. This recommended mesh size is calculated based on the fact that shrimp with CL = 9.39 and 12.72 will have a total length of 49.07 and 63.78 mm (TL = 7.5678 + 4.4194CL; Tzeng et al., 2005). Then, the 50% catch efficiency for thick-shelled shrimp is estimated by the equation $L0.5 = 4.2500Me - 90.0250$ [where L = total length (in mm) and Me = mesh size (in mm)]. Accordingly, the best mesh size for 50% catch capability is 32.7–36.2 mm. However, for conservation purposes, here, we suggest using a larger mesh size to lower the catch percentage of the first mature shrimp. This would insure that the fishermen catch and sell the larger shrimp to make a good profit while also sustaining the valuable shrimp resources.

Conclusion

Metapenaeopsis palmensis is a stenohaline species inhabiting a water depth no deeper than 40 m, with a bathymetric distribution in relation to their size. The intraspecific size segregation, whereby the adults and subadults live in shallower water (10–20 m) and the newly recruited juveniles stay in deeper water (25–35 m), is highly correlated to the local environmental characteristics. They are multiple spawners with a spawning season of almost half a year in line with the natural water temperature. They spawn from February to June when the water temperature (25°C) is appropriate, and reveal a shorter spawning period with the increase in latitude. Based on the results of reproduction, recruitment patterns, and environmental conditions obtained in this study, we suggest that only the late reproduced *M. palmensis* (May–June) can recruit successfully in large numbers. This is an important information for resource conservation and management to set fishing regulations, e.g., banning shrimp trawling in May and June, and restricting the smallest mesh size of cod net to 4 cm, for the sustainability of local fisheries.

References

Aktaş, M., M. Kumlu & O. T. Eroldoğan, 2003. Off-season maturation and spawning of *Penaeus semisulcatus* by eyestalk ablation and/or temperature–photoperiod regimes. Aquaculture 228: 361–370.

Aragón-Noriega, E. A. & E. Alcántara-Razo, 2005. Influence of sea surface temperature on reproductive period and size at maturity of brown shrimp (*Farfantepenaeus californiensis*) in the Gulf of California. Marine Biology 146: 373–379.

Chen, H. S., 2006. Assemblages of Epibenthic Shrimps in Coastal Waters off Southwestern Taiwan. M.S. Thesis, Department of Marine Biotechnology and Resources, National Sun Yat-sen University. (In Chinese with English abstract).

Chen, C. T. A., J. T. Liu & B. J. Tsuang, 2004. Island-based catchment: the Taiwan example. Regional Environmental Change 4: 39–48.

Clark Jr., W. H., J. W. Lynn, A. I. Yudin & H. O. Persyn, 1980. Morphology of the cortical reaction in the eggs of *Penaeus aztecus*. Biological Bulletin 185: 175–186.

Courtney, A. J., J. M. Masel & D. J. Die, 1995. Temporal and spatial patterns in recruitment of three penaeid prawns in Moreton Bay, Queensland, Australia. Estuarine, Coastal and Shelf Science 41: 377–392.

Criales, M. M., M. J. Bello & C. Yeung, 2000. Diversity and recruitment of Penaeoid shrimps (Crustacea: Decapoda) at Bear Cut, Biscayne Bay, Florida, USA. Bulletin of Marine Science 67(2): 773–788.

Crocos, P. J. & J. D. Kerr, 1986. Factors affecting induction of maturation and spawning of the tiger prawn, *Penaeus esculentus* (Haswell), under laboratory conditions. Aquaculture 58(3/4): 203–214.

Dadson, S. J., N. Hovius, H. Chen, W. B. Dade, M. L. Hsieh, S. D. Willett, J. C. Hu, M. J. Horng, M. C. Chen, C. P. Stark, D. Lague & J. C. Lin, 2003. Links between erosion, runoff variability and seismicity in the Taiwan orogen. Nature 426: 648–651.

Dall, W., B. J. Hill, P. C. Rothlisberg & D. J. Sharples, 1990. The Biology of the Penaeidae. In Blaxter, J. H. S. & A. J. Southward (ed.), Advances in Marine Biology, Vol. 27. Academic Press, London.

De Grave, S., N. D. Pentcheff, S. T. Ahyong, T.-Y. Chan, K. A. Crandall, P. C. Dworschak, D. L. Felder, R. M. Feldmann, C. H. J. M. Fransen, L. Y. D. Goulding, R. Lemaitre, M. E. Y. Low, J. W. Martin, P. K. L. Ng, C. E. Schweitzer, S. H. Tan, D. Tshudy & R. Wetzer, 2009. A classification of living and fossil genera of decapod crustaceans. Raffles Bulletin of Zoology Supplement 21: 1–109.

Diaz, R. J., 2001. Overview of hypoxia around the world. Journal of Environmental Quality 30: 275–281.

Gammelsrød, T., 1992. Variation in shrimp abundance on the Sofala Bank, Mozambique, and its relation to the Zambezi River runoff. Estuarine, Coastal and Shelf Science 35: 91–103.

Hayashi, K. I. & T. Sakamoto, 1978. Taxonomy and biology of *Metapenaeopsis palmensis* (Haswell) (Crustacea, Decapoda, Penaeoideae) collected from the Kii Strait, central Japan. Bulletin of the Japanese Society of Scientific Fisheries 44: 709–714.

Hoang, T., S. Y. Lee, C. P. Keenan & G. E. Marsden, 2002. Effect of temperature on spawning of *Penaeus merguiensis*. Journal of Thermal Biology 27: 433–437.

Holthuis, L. B., 1980. FAO Species Catalogue. Volume 1: Shrimp and Prawns of the World. An Annotated Catalogue of Species of Interest to Fisheries. FAO Fisheries Synopsis, Rome: xvii + 271 pp.

Hossain, M. Y. & J. Ohtomi, 2008. Reproductive biology of the southern rough shrimp *Trachysalambria curvirostris* (Penaeidae) in Kagoshima Bay, southern Japan. Journal of Crustacean Biology 28: 607–612.

Kruevaisayawan, H., R. Vanichviriyakit, W. Weerachatyanukul, B. Withyachumnarnkul, J. Chavadej & P. Sobhon, 2010. Oogenesis and formation of cortical rods in the black tiger shrimp, *Penaeus monodon*. Aquaculture 301: 91–98.

Kumlu, M., D. Avşar, T. Eroldoğan & N. Başusta, 1999. Some biological aspects of penaeid shrimps inhabiting Yumurtalık Bight in İskenderun Bay (North-Eastern Mediterranean). Turkish Journal of Zoology 23: 53–59.

Kumlu, M., S. Türkmen, M. Kumlu & O. T. Eroldoğan, 2011. Off-season maturation and spawning of the Pacific white shrimp *Litopenaeus vannamei* in sub-tropical conditions. Turkish Journal of Fisheries and Aquatic Sciences 11: 15–23.

Lee, D. A., T. Y. Chan, H. P. Yu & I. C. Liao, 1999. A revised checklist of the penaeoidea (Crustacea: Decapoda) from the waters around Taiwan. The Raffles Bulletin of Zoology 47: 441–447.

Lin, H., G. Charmantier, P. Thuet & J. Trilles, 1992. Effect of turbidity on survival, osmoregulation and gill Na$^+$–K$^+$ ATPase in juvenile shrimp *Penaeus japonicus*. Marine Ecology Progress Series 90: 31–37.

Linke, T. E., M. E. Platell & I. C. Potter, 2001. Factors influencing the partitioning of food resources among six fish species in a large embayment with juxtaposing bare sand and seagrass habitats. Journal of Experimental Marine Biology and Ecology 266: 193–217.

Liu, C. C., C. H. Chang, C. G. Wen, C. H. Huang, J. J. Hung & J. T. Liu, 2009. Using satellite observation of ocean color to categorize the dispersal patterns of river-borne substances in the Gaoping (Kaoping) River, Shelf and Canyon system. Journal of Marine System 76: 496–510.

Liu, J. P., C. S. Liu, K. H. Xu, J. D. Milliman, J. K. Chiu, S. J. Kao & S. W. Lin, 2008. Flux and fate of small mountainous rivers derived sediments into the Taiwan Strait. Marine Geology 256: 65–76.

Milliman, J. D. & J. P. M. Syvitski, 1992. Geomorphic/tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers. The Journal of Geology 100: 525–544.

Ohtomi, J. & T. Matsuoka, 1998. Reproduction and growth of Jack-knife shrimp, *Haliporoides sibogae*, off south western Kyushu, Japan. Fisheries Research 38: 271–281.

Pechenik, J. A., 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Marine Ecology Progress Series 177: 269–297.

Pianka, E. R., 1970. On r- and K-selection. The American Naturalist 104: 592–597.

Potter, I. C., F. M. Baronie, R. J. G. Manning & N. R. Loneragan, 1989. Reproductive biology and growth of the western school prawn, *Metapenaeus dalli*, in a large western Australian estuary. Australian Journal of Marine & Freshwater Research 40: 327–340.

Raymundo-Huizar, A., H. Perez-Espana, M. Mascaro & X. Chiappa-Carrara, 2005. Feeding habits of the dwarf weakfish (*Cynoscion nannus*) off the coasts of Jalisco and Colima, Mexico. Fisheries Bulletin 103: 453–460.

Riera, P., P. A. Montagna, R. D. Kalke & P. Richard, 2000. Utilization of estuarine organic matter during growth and migration by juvenile brown shrimp *Penaeus aztecus* in a South Texas estuary. Marine Ecology Progress Series 199: 205–216.

Sakaji, H., 2001. Observation of the oocytes of the small penaeid shrimps *Metapenaeopsis aegyptia*, *M. barbata*, and *M. sinica*. Benthos Research 56(2): 81–85.

Sakaji, H., 2003. Fishery biological studies on penaeid shrimps in Tosa Bay, Pacific coast of Japan. Bulletin of Fisheries Research Agency 6: 73–127. (In Japanese with English abstract).

Sakaji, H., K. Tsuchiya & S. Segawa, 2000. Oocyte development of *Metapenaeopsis dalei* (Penaeidae, Decapoda, Crustacea). Invertebrate Reproduction and Development 38: 7–12.

Sakamoto, T. & K. Hayashi, 1977. Prawn and shrimps collected from the Kii Strait by small type trawlers. Bulletin of the Japanese Society of Scientific Fisheries 43: 1259–1268. (In Japanese with English abstract).

Tzeng, T. D., C. S. Chiu & S. Y. Yeh, 2005. Growth and mortality of the red-spot prawn (*Metapenaeopsis barbata*) in the Northeastern Taiwan. Journal of Fishery Society of Taiwan 32: 229–238.

Villalobos-Rojas, F. & I. S. Wehrtmann, 2011. Gonad development in the commercially exploited deepwater shrimp *Solenocera agassizii* (Decapoda: Solenoceridae) from Pacific Costa Rica, Central America. Fisheries Research 109: 150–156.

Watson, R. A. & J. A. Keating, 1989. Velvet shrimp (*Metapenaeopsis* spp.) of Torres Strait, Queensland, Australia. Asian Fisheries Science 3: 45–56.

Yamada, R., K. Kodama, T. Yamakawa, T. Horiguchi & I. Aoki, 2007. Growth and reproductive biology of the small penaeid shrimp *Trachysalambria curvirostris* in Tokyo Bay. Marine Biology 151: 961–971.

Yano, I., 1988. Oocyte development in the kuruma prawn *Penaeus japonicus*. Marine Biology 99: 547–553.

Yano, I., 1995. Final oocyte maturation, spawning and mating in penaeid shrimp. Journal of Experimental Marine Biology and Ecology 193: 113–118.