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Reproductive Biology of the Redtail Prawn, *Penaeus penicillatus*, in the Southwestern Waters of Taiwan

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ABSTRACT

The redtail prawn, *Penaeus penicillatus*, is commercially important for bottom trawling and shrimp beam trawling in the southwestern waters of Taiwan. However, no histological study of this species based on wild samples has been conducted. In this work, the reproductive biology of *P. penicillatus* was studied based on monthly samples collected in the southwestern waters of Taiwan from December 2020 to December 2021. The total length (TL) ranged from 84.5 to 253.3 mm for 634 females, while body weight (BW) varied from 7.2 to 140.2 g. For 956 males, minimum and maximum sizes were 78.3 and 181.7 mm TL, respectively, while BW ranged from 6.0 to 53.9 g. The relationship between TL and BW was BW = 8.0×10^{-5} $TL^{2.61}$ (R^2 = 0.93, n = 1,590), and there were no statistically significant differences between females and males. The overall sex ratio was 0.40 (X^2= 65.21, p < 0.001), but females were significantly more common among individuals larger than 165 mm TL. In addition, monthly sex ratios fluctuated from 0.19 to 0.51 without a systematic pattern. Reproductive activity, assessed using histology and the gonadosomatic index (GSI), indicated that mature females could be found during February to May and August to November, with peak spawning occurring from February to May. For females, the minimum size at maturity and estimated length at 50% maturity were 87.3 mm TL and 169.3 mm TL, respectively.

Key words: *Penaeus penicillatus*, length at maturity, gonadosomatic index, spawning season

INTRODUCTION

The redtail prawn, *Penaeus penicillatus* (Alcock, 1905), is widely distributed in the tropical and subtropical waters of the Indo-West Pacific region. It inhabits coastal waters of southwestern Taiwan and has a bathymetric distribution ranging from depths of 2 to 90 m (Yu and Chan, 1986; Taiwan Large Crustacean Database, 2022). *P. penicillatus* is commercially important for small-scale bottom trawling and shrimp beam trawling in the southwestern waters of Taiwan. In addition, there were previous attempts of artificial breeding of *P. penicillatus* for aquaculture (Liao, 1988; Miao, 1992; Miao, 1995). However, in captivity the growth rate declines rapidly when the shrimp reaches 10 cm (Chen *et al*., 1988).

Li (1990) studied ovarian development and steroid concentrations of *P. penicillatus* from Taiwanese waters in captivity. Lin (1989) confirmed that the populations of *P. penicillatus* in the southwestern waters of Taiwan (Donggang, Kaohsiung, and Chiayi) belonged to the same unit stock. For *P. penicillatus* populations in waters along the Pakistani coast of the Arabian Sea, two spawning peaks were reported on the basis of ovary color and histology (Ayub and Ahmed, 2002). Moreover, sexual maturity was attained when *P. penicillatus* reached 66 to 70 mm in length in Indian waters of the Arabic Sea (Patel *et al*., 2011).

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The shrimp fishery is important in the coastal waters of southwestern Taiwan. However, the information available on the reproductive biology of *P. penicillatus* is too scarce to permit sustainable management and exploitation of this resource in the waters of Taiwan. Consequently, the lack of adequate knowledge of its reproductive biology remains an impediment to proper management and conservation. Therefore, the present study describes the reproductive biology of *P. penicillatus* from the southwestern waters of Taiwan in relation to ovarian maturation, size at maturity, and spawning season.

MATERIALS AND METHODS

1. Sampling and Measurements

Monthly samples were randomly collected by commercial bottom trawling and shrimp beam trawling at Dongshi fishing harbor in Chiayi County from December 2020 to December 2021. No samples were available in June 2021 due to the quarantine measures in Taiwan. The specimens were sexed according to the presence of a petasma for males and a thelycum for females. The total length (TL) was measured from the posterior margin of the orbit notch of the carapace to the end of the telson to the nearest 0.1 mm. Body weight (BW) and gonad weight (GW) were measured to the nearest 0.01 g. A subset of samples was selected, and the ovaries of these specimens were removed, measured, and fixed with 10% formalin for further histological analysis.

2. Data Analysis

(1) Gonadosomatic index

The gonadosomatic index (GSI) was determined for each individual female by following the methods of Uosaki and Bayloff (1999) and Armas *et al*. (2006):

GSI = (GW/female BW) × 100

(2) Macroscopic staging of ovarian maturity

Ovarian development was determined visually and categorized into four consecutive stages based on the macroscopic ovarian staging of Motoh (1978) and Li (1990):

A. Undeveloped stage

Ovaries are very thin and small relative to other organs. They are translucent and very flaccid. Oocytes are at the oogonial stage or chromatin nucleolar stage.

B. Developing stage

Developing ovaries can easily be distinguished from other tissues. They are larger than undeveloped ovaries. Fresh ovaries are cream white. Oocytes are at the perinucleolar stage to the pre-yolk stage.

C. Nealy ripe stage

Ovaries are large and turgid. Fresh ovaries are buff to yellow. Oocytes are at the yolk globular stage.

D. Ripe stage

Ovaries are at full size and are rigid and green to dark green. Oocytes are at the early cortical alveolar stage to the late cortical alveolar stage.

Subsequently, the proportions of specimens in each stage in each month were illustrated to reveal the temporal development of the ovaries of females.

(3) Histological analysis of ovaries

The performance of macroscopic staging based on the appearances of ovaries and the GSI in assessing ovarian maturity status was verified by histological examination. The processing of the ovaries, including dehydration, clearing, infiltration, and embedding, followed that of Humason (1967) and Ayub and Ahmed (2002). The ovaries embedded in paraffin were sliced into 5 μm sections and then stained with hematoxylin and counter-stained with eosin, cover-slipped with a mounting medium, and examined under a microscope. Previous studies found no difference in maturation stage with respect to ovary position (Niamaimandi *et al.*, 2008; Rahman and Ohtomi, 2020). Therefore, tissue samples extracted from the anterior regions of the abdominal lobes were used for further histological analysis to determine the developmental stages of the oocytes.

Additionally, the mean diameters of oocytes were determined from measurements of the histological

Table 1 Specimens of *Penaeus penicillatus* collected from December 2020 to December 2021 in the southwestern waters of Taiwan

Year	Month	Female			Male			Total
		N	Range of TL (mm)	Range of BW (g)	N	Range of TL (mm)	Range of BW (g)	
2020	Dec.	97	107.7-253.3	14.2-140.2	157	118.7-178.8	20.1-51.7	254
2021	Jan.	55	140.9-191.1	35.0-77.0	90	138.7-164.5	31.0-48.3	145
	Feb.	59	129.6-203.4	25.2-99.9	82	128.2-164.0	23.3-53.9	141
	Mar.	51	122.2-189.8	20.0-85.0	117	107.1-163.5	14.1-52.6	168
	Apr.	78	106.7-195.2	13.1-88.5	77	121.9-181.7	14.3-48.4	155
	May	11	99.8-194.7	11.9-82.3	48	107.5-156.3	15.1-44.2	59
	Jun.	0	–	–	0	–	–	0
	Jul.	40	98.9-151.3	9.6-40.7	54	92.9-141.3	8.9-30.7	94
	Aug.	65	84.5-151.4	7.2-50.1	103	78.3-125.7	6.0-29.9	168
	Sep.	44	112.8-200.0	15.4-93.8	43	100.5-152.5	11.4-39.5	87
	Oct.	42	104.9-162.4	15.2-56.5	71	116.5-149.0	20.5-49.0	113
	Nov.	40	115.2-164.1	28.1-73.8	40	111.8-148.9	26.3-46.6	80
	Dec.	52	95.8-171.0	12.0-84.9	74	90.4-153.6	11.9-46.7	126
Total		634	84.5-253.3	7.2-140.2	956	78.3-181.7	6.0-53.9	1590

N, sample number; TL, total length; BW, body weight

samples at different ovarian stages. For each stage, 10 to 25 samples were chosen, and 3 to 6 oocytes were measured for each sample; the measurements of all oocytes were then averaged to represent the mean diameter of oocytes of a given stage.

(4) Sex ratio

The sex ratio (%) was determined by counting the numbers of males and females by month and by size classes and assessing them using a chi-squared (χ^2) test.

Sex ratio = the number of females / (the numbers of females + males) × 100%

(5) Length at 50% maturity

The length at maturity is defined as the length at which the ovaries are in the developing stage, the nearly ripe stage, or the ripe stage according to the GSI. Minimum size at maturity was determined by directly comparing ovary maturation stage with TL. The length at which 50% of all individuals were mature was determined by modeling the size-specific proportion of mature ovaries in each 15 mm TL class. A conventional logistic equation as described by King (1995) was used to quantify such a relationship:

$Pr = 1/(1 + e^{a+b\mathrm{TL}})$

Pr: Proportion of mature individuals in a size class

TL: Total length

a, b: Constants

RESULTS AND DISSCUSSION

1. Sex Ratio

From December 2020 to December 2021, a total of 1,590 specimens of *P. penicillatus* were collected, of which 634 were female and 956 were male. The TL ranged from 84.5 to 253.3 mm for females, while BW varied from 7.2 to 140.2 g (Table 1). For males, minimum and maximum sizes were 78.3 and 181.7 mm TL, respectively, while BW varied from 6.0 to 53.9 g.

Monthly variation in sex ratio is described in Table 2. The overall sex ratio during the sampling period was 0.40, which differed significantly from 0.5 (χ^2 = 65.21, p < 0.001). In addition, the monthly sex

Table 2 Monthly sample sizes of female and male *Penaeus penicillatus* collected from December 2020 to December 2021 in the southwestern waters of Taiwan

Year	Month	Female	Male	Sex ratio (%)	χ^2	*p*-value
2020	Dec.	97	157	0.38	14.17	0.00017*
2021	Jan.	55	90	0.38	8.45	0.00365*
	Feb.	59	82	0.42	3.75	0.05275
	Mar.	51	117	0.30	25.93	0.00000*
	Apr.	78	77	0.50	0.01	0.93598
	May	11	48	0.19	23.20	0.00000*
	Jun.	0	0	–	–	–
	Jul.	40	54	0.43	2.09	0.14874
	Aug.	65	103	0.39	8.60	0.00337*
	Sep.	44	43	0.51	0.01	0.91462
	Oct.	42	71	0.37	7.44	0.00637*
	Nov.	40	40	0.50	0.00	1.00000
	Dec.	52	74	0.41	3.84	0.05001
Total		634	956	0.40	65.21	0.00000*

Sex ratio is the percentage of females in monthly or total samples. Asterisks indicate statistical significance of chi-square (χ^2) tests at $p < 0.05$.

Table 3 Sample sizes of female and male *Penaeus penicillatus*, grouped by size class, collected from December 2020 to December 2021 in the southwestern waters of Taiwan

Length (mm)	Female	Male	Sex ratio (%)	χ^2	*p*	Length (mm)
75	0	0	–	–	–	75
90	3	4	42.3	0.14	0.7055	90
105	7	33	20.5	15.36	0.0001*	105
120	54	131	29.3	36.53	*p*<0.05*	120
135	85	178	32.1	43.45	*p*<0.05*	135
150	118	181	41.2	11.65	0.0006*	150
165	111	254	33.6	41.68	*p*<0.05*	165
180	93	60	61.8	8.72	0.0031*	180
195	54	1	98.2	51.07	*p*<0.05*	195
210	15	0	100	15.00	0.0001*	210
225	1	0	100	1	0.3173	225
240	0	0	–	–	–	240
255	1	0	100	1.00	0.3173	255

Sex ratio is the percentage of females in monthly or total samples. Asterisks indicate statistical significance of chi-square (χ^2) tests at $p < 0.05$.

ratios fluctuated from 0.19 to 0.51 without a systematic pattern. Males were more abundant in most months except for April, September, and November. The proportions of males were significantly higher for size classes under 180 mm TL (Table 3), and the proportions of females increased with TL when TL was greater than 180 mm. The proportions of females were significantly higher in larger size classes.

For *Penaeus semisulcatus* in Australia, the sex ratio within the same year class remains at around 1:1 from the time of recruitment to about 1 year of age. Subsequently, the percentage of females declines steadily. At the age of approximately 18 months, females account for only about 25% of the population (Somers and Kirkwood, 1991). For *Penaeus monodon* in southeast Asia, the female to male ratio was higher

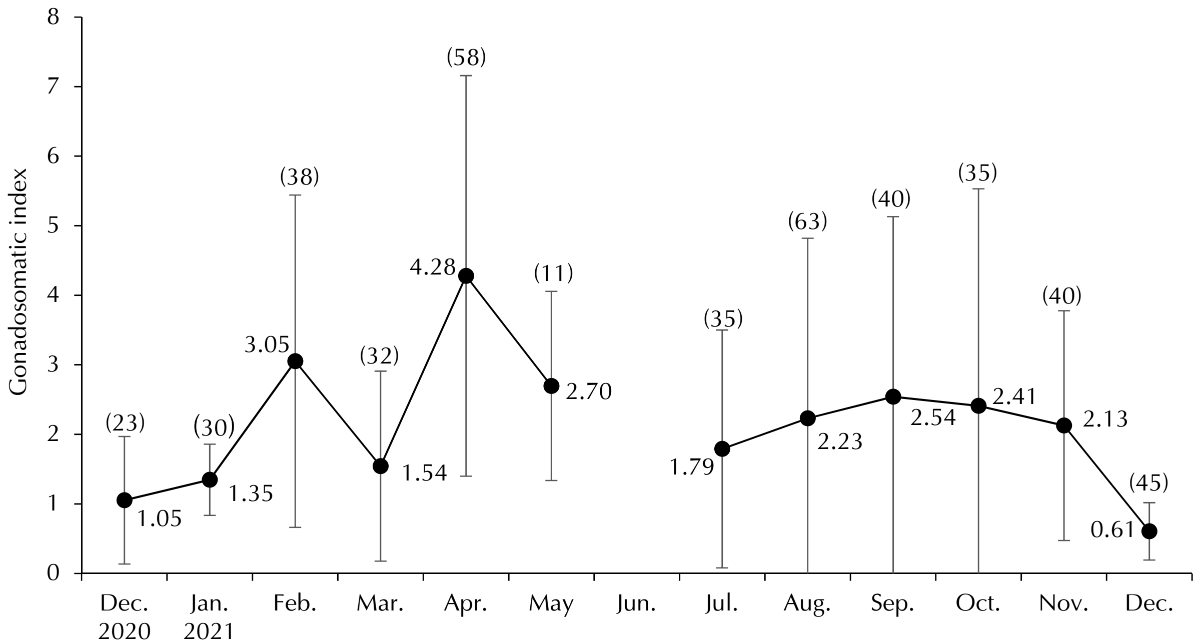

Fig. 1 Monthly changes in the mean gonadosomatic index for female *Penaeus penicillatus* (*N* = 450) in the southwestern waters of Taiwan. Sample sizes are noted in parentheses.

in offshore waters (1.5) than in the nursery areas (1.0) (Motoh, 1984). Because the life history of *P. monodon* contains six phases, i.e., embryo, larva, juvenile, adolescent, subadult, and adult, habitat and ecology change with each stage (Motoh, 1984). The sex ratio may differ among life stages, habitats, and fishing gear used. In this study, the observed sex ratio represents the pattern from samples collected by commercial bottom trawling and shrimp beam trawling in fishing areas located in offshore waters. In the future, more studies of the variation in sex ratio are greatly needed.

2. GSI Variation

Among the 634 female samples, a total of 450 ovaries were successfully removed for GSI measurements. For smaller individuals, some of the ovaries were too small to observe or measure and were excluded from GSI analysis. GSI measurements ranged from 0.61 to 4.28. The GSI remained low in December 2020 and January 2021. It rose from 3.05 in February to a peak of 4.28 in April, slightly decreased in May and July (no samples in June), and increased thereafter to 2.23 in August then decreased to 2.13 in November (Fig. 1). The GSI dropped substantially to a low of 0.61 in December 2021.

3. Developmental Stages of Oocytes

Among the 450 ovaries removed, 120 samples were randomly selected for further histological analysis. Based on previous studies (Li, 1990; Ayub and Ahmed, 2002; Niamaimandi *et al.*, 2008), seven oogenesis stages were defined for *P. penicillatus* using microscopic characteristics (Fig. 2). Descriptions are as follows:

(1) Oogonial stage

Oocytes were small (<0.02 mm) and could not be distinguished easily (Fig. 2A). Chromatin was dyed deep purple by hematoxylin. (Sample size (*N*) = 10; 3 oocytes were measured for each sample).

(2) Chromatin nucleolar stage

Chromatin nucleolar cells (0.02-0.04 mm) contained a thin layer of cytoplasm and a large nucleus (Fig. 2B). (*N*=10; 3 oocytes were measured for each sample).

(3) Perinucleolar stage

Perinucleolar oocytes were large (0.04-0.05 mm), and the cytoplasmic region was clear (Fig. 2C). The

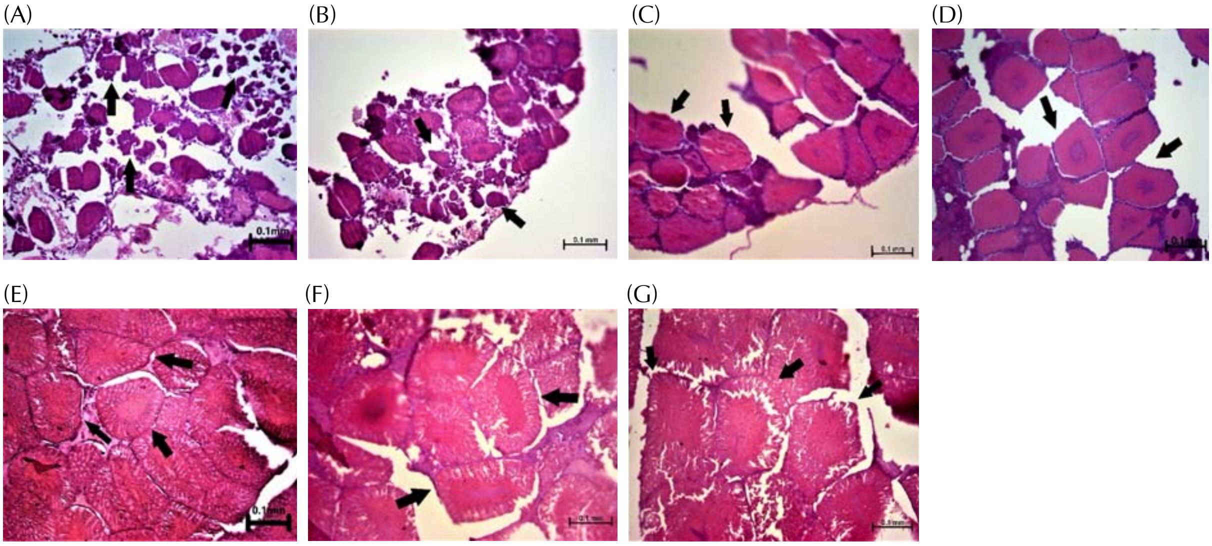

Fig. 2 Histological sections of the ovaries of *Penaeus penicillatus*, illustrating oocytes at different maturation stages. (A) Oogonial stage, (B) chromatin nucleolar stage, (C) perinucleolar stage, (D) pre-yolk stage, (E) yolk globular stage, (F) early cortical alveolar stage, and (G) late cortical alveolar stage.

nucleus was well-formed. (*N* = 15; 3 oocytes were measured for each sample).

(4) Pre-yolk stage

Oocytes had continued to grow larger (0.05-0.09 mm) and were oval in shape (Fig. 2D). The nucleus had a clear nuclear membrane. Follicle cells were visible on the outer surfaces of the oocytes. (*N* = 20; 4 oocytes were measured for each sample).

(5) Yolk globular stage

Yolk granules were present in the cytoplasmic region (Fig. 2E). Each oocyte (0.08-0.19 mm) was surrounded by a layer of elongated follicle cells, which were less distinguishable. (*N* = 20; 6 oocytes were measured for each sample).

(6) Early cortical alveolar stage

The follicle cells on the outer layer of the oocytes became even thinner (Fig. 2F). The rod-shaped cortical bodies (0.005-0.008 mm in diameter) were observed at the inner periphery of oocytes. Oocytes were larger than 0.19 mm. (*N* = 25; 6 oocytes were measured for each sample).

(7) Late cortical alveolar stage

The cortical bodies in the chromatin of oocytes had grown larger (>0.03 mm). Follicle cells enveloping the oocytes with cortical bodies were not distinguishable (Fig. 2G). (*N* = 20; 6 oocytes were measured for each sample).

4. Ovarian Development

The maturity of the ovary of was determined by its shape and coloration, variation in the GSI, and histological study. The GSI values and oocyte diameters are described below:

(1) Undeveloped stage

The GSI was less than 0.7. The oocyte diameter ranged from 0.01 to 0.04 mm.

(2) Developing stage

The GSI ranged from 0.8 to 1.6. Oocytes generally ranged from 0.04 to 0.09 mm in diameter.

(3) Nealy ripe stage

The GSI ranged from 1.7 to 3.9. The oocyte diameter ranged from 0.09 to 0.19 mm.

(4) Ripe stage

The GSI was greater than 3.9, and oocytes were larger than 0.19 mm.

The proportions of specimens in each maturation

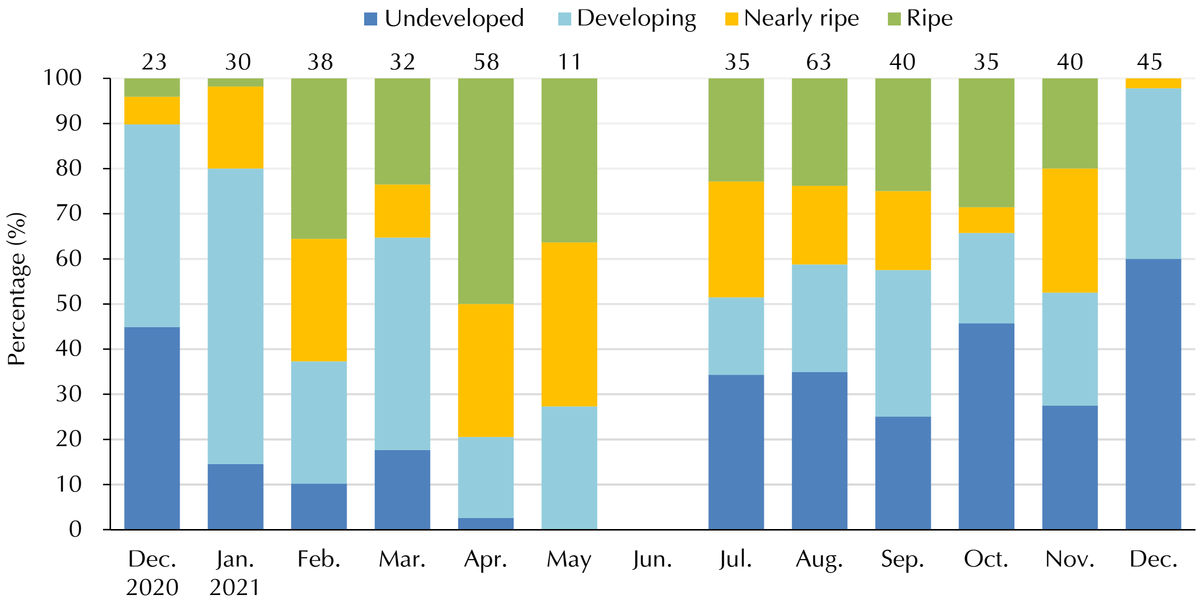

Fig. 3 Monthly variation in the proportions of females in different ovarian maturation stages for *Penaeus penicillatus* in the southwestern waters of Taiwan. Sample sizes are illustrated above each bar.

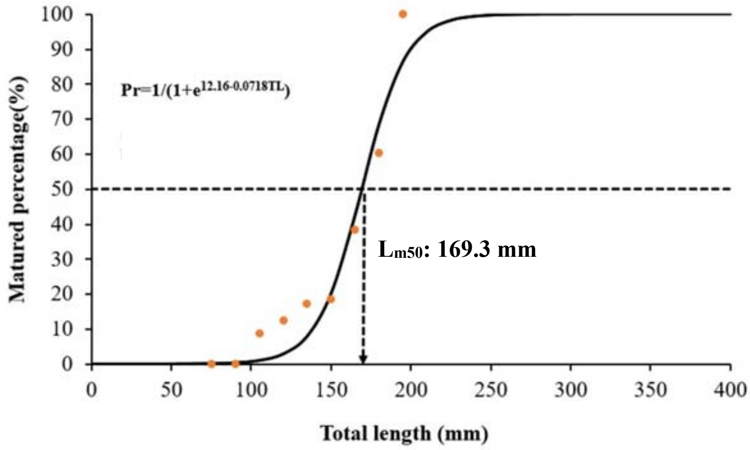

Fig. 4 Relationship between the percentage of mature individuals and total length for female *Penaeus penicillatus* collected in the southwestern waters of Taiwan. Length at 50% maturity (Lm_{50}) is indicated by dashed lines.

stage in each month were illustrated to reveal the temporal development of female ovaries (Fig. 3). In December 2020, individuals with ovaries in the ripe stage occurred at a low percentage (4.1%). The percentage of ovaries in the ripe stage increased sharply in February (35.6%), was highest in April (50%), and remained high until May (36.4%). Ripe individuals could be found from July through November. The percentages of ovaries in the undeveloped stage also increased from July to November. In December 2021, individuals in the ripe stage were absent. Overall, ovarian development corresponded well with the monthly changes in the GSI and the percentages of individuals in the various maturation stages (Figs. 1, 3).

5. Size at Maturity

The smallest mature female, as determined by macroscopic analysis of the ovary, found in this study was 87.3 mm TL. A total of 450 females ranging from 84.5 to 253.3 mm TL were used to estimate size at maturity. The changes in the proportions of mature females in 15 mm TL size intervals were described by the following logistic curve:

$$Pr = 1/(1 + e^{12.16-0.0718TL})$$

Therefore, the length at 50% maturity (L_{m50}) was estimated to be 169.3 mm TL (Fig. 4).

The development of gonads is a continuous and consecutive progress. Determination of the ovarian maturation stage is difficult by visual examination of the ovaries alone (Ohtomi *et al*., 2003). Hence, the histological observation of oocytes is believed to be the most accurate method for the staging of mature females (Ohtomi *et al*., 2003; Hossain and Ohtomi, 2008). In this study, both methods were adopted to describe the detailed ovarian development of *P. penicillatus* in the southwestern waters of Taiwan.

Among the 11 *Penaeus* species in Taiwan, *P. japonicus*, *P. monodon*, *P. semisulcatus*, and *P. penicillatus* are large and commonly utilized by fisheries (Lee, 2005). However, past studies have focused more on physiology and aquaculture. As a result, information on the reproductive biology of wild *Penaeus* populations in the waters of Taiwan is still lacking. In this study, we estimated the minimum size at maturity and length at 50% maturity to be 87.3 mm and 169.3 mm TL, respectively. Patel *et al.* (2011) estimated that the minimum size at maturity was 66 mm TL in Indian waters. Moreover, the minimum size at maturity was estimated to be 123 mm TL for *P. penicillatus* in Pakistani waters (Ayub and Ahmed, 2002). As growth rates of penaeid shrimps are greatly influenced by environmental factors, such as water temperature, prey, and seasonality (Miao and Tu, 1995; Rahman and Ohtomi, 2018; Rahman and Ohtomi, 2020), the size at maturity for *P. penicillatus* may vary among geographic regions.

6. Spawning Season

The GSI of *P. penicillatus* was highest from February to May (Fig. 1) and remained high until November. The GSI dropped to a low of 0.61 in December 2021. Moreover, the proportions of specimens at different maturation stages for each month also showed that ripe individuals could be found from February to November (Fig. 3), with the highest percentages from February to May. In summary, we found that the monthly changes in the GSI corresponded well with the maturation stages of the ovary. Ayub and Ahmed (2002) reported that the spawning of *P. penicillatus* in waters of the Arabic Sea showed a bimodal pattern. One period of egg laying occurred from February to May, and the other occurred from July to November. Another study revealed that the main spawning season was from March to May along the Guangdong coastal waters of China (Wang *et al.*, 2021). In conclusion, this study found that mature females of *P. penicillatus* in the southwestern waters of Taiwan could be found during a prolonged spawning season, from February to May and from August to November, and that the peak spawning season occurred from February to May.

Studying the reproductive biology of *P. penicillatus* is crucial for sustainable fishery management practices. Understanding factors like spawning seasons, spawning areas, and reproductive potential aids in setting appropriate fishing quotas and regulations. To prevent overexploitation, fishing pressure should be reduced during the peak spawning season. In the future, more studies on the life history of *P. penicillatus* populations are needed to design effective conservation strategies.

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臺灣西南海域長毛對蝦 (*Penaeus penicillatus*) 之生殖生物學研究

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摘　要

長毛對蝦 (*Penaeus penicillatus*) 為臺灣西南海域單船拖網及蝦桁拖網漁業重要經濟物種之一，然相關基礎調查資料仍闕如，本研究目的即為建立其生殖生物學參數，俾利未來進行管理之用。調查期間由 2020 年 12 月起至 2021 年 12 月止，按月至嘉義東石漁港採樣，共採集雌蝦 634 尾，雄蝦 956 尾，共計 1,590 尾樣本，總性比為 0.4，雌雄比例存在顯著差異。雌蝦體長介於 84.5 – 253.3 mm，雄蝦則為 78.3 – 181.7 mm；雌蝦體重介於 6.04 – 253.85 g，雄蝦則為 7.21 – 140.16 g，體長與體重之關係式為 $BW = 8.0 \times 10^{-5}\ TL^{2.61}$ ($R^2 = 0.93$，n=1,590)；根據卵巢生殖腺外觀及生殖腺指數月別變動，同時參考卵巢組織切片等數據，推估長毛對蝦有兩個生殖期，一為 2 – 5 月，其次為 8 – 11 月，高峰在 2 – 5 月。雌蝦最小性成熟體長為 87.3 mm，50% 性成熟體長為 169.3 mm。

關鍵詞：長毛對蝦、*Penaeus penicillatus*、性成熟體長、生殖腺指數、生殖季節

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