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RESEARCH ARTICLE

Reproductive biology of the spiny lobster, *Panulirus Penicillatus*, in the southeastern coastal waters off Taiwan

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Abstract The reproductive biology of spiny lobster, *Panulirus penicillatus*, was studied based on 2,068 lobsters, ranging from 34.28 to 131.60 mm carapace length (CL), sampled in Taitung coastal waters from September 2003 to December 2004. The overall sex ratio approximated 1:1 ($\chi^2 = 0.02, P > 0.05$), but the monthly sex ratios in 2004 showed significant differences and males were predominant in sizes larger than 80 mm CL. Reproductive activity, assessed using histology, a gonadosomatic index and percentage of ovigerous females, indicated that the mature females could be found in every month and that the major spawning occurred from May to September. The presence of re-developing/re-ripe ovaries by month and size-specific spawning time suggest that larger mature females (>60 mm CL) spawn at least three times a year while smaller new mature females spawn at least once a year. For females, the estimated sizes at 50% physiological and functional maturity were (mean ± SE) 56.46 ± 0.56 mm CL and 66.63 ± 1.07 mm CL. The estimated sizes at functional maturity were between 72 and 74 mm CL for males. The number of eggs per spawning event (brood size, BS) was related to CL by the equation $Y_{\mathrm{BS}} = 2.4 \times 10^{-3}\ \mathrm{CL}^{4.18}$ ($r^2 = 0.902$, $n = 12$). Female lobsters with CL ranging from 60 to 80 mm made the greatest contributions to egg production because of their high brood size and active reproductive activity. A minimum legal size should be established for the fishery to protect egg production potential of lobster population in the southeastern coastal waters off Taiwan.

Keywords *Panulirus penicillatus* · Taitung · Ovarian development · Spawning time · Size at maturity · Brood size · Relative reproductive potentials

Introduction

The spiny lobster, *Panulirus penicillatus*, is widely distributed in the Indo-West Pacific. It is a shallow water species and mainly inhabits the upper 4–5 m on outer reef slopes in the tropical Pacific (George 1972). The spiny lobster is an important commercial species in the southeastern coastal water off Taiwan (Taitung), where it is caught by skin-diving or trammels net throughout the year. The spiny lobster fishery is managed with a minimum size limit of 20 cm total length or about 73.07 mm carapace length (CL) for all species along the coast of Taiwan (Taiwan Provincial Government 1987). However, this regulation is not derived from any consideration of reproductive biology and other life history processes and has not been strictly enforced. Small lobsters or berried females were common in the fish markets. This lack of protection of spawners could damage reproductive potential of the lobster population, resulting in recruitment failure and

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overexploitation. In fact, the average size of the lobster population has been seen decreasing over the last decade.

Despite the importance of the *P. penicillatus* fisheries in the Indo-West Pacific, information about its key life history parameters is limited. Its reproductive biology (i.e., size at maturity and brood size) has been previously studied for the *P. penicillatus* population in Hawaii (Morris 1968; McGinnis 1972; MacDonald 1979), Palau (MacDonald 1988), Philippines (Junio 1987) and Red sea (Plaut 1993; Hogarth and Barratt 1996). However, all these studies except for Junio (1987) only used the external morphological indicators such as berried conditions to determine the maturity and provided no estimates of size at physiological maturity and macroscopic description of ovarian development. Large variations in reproductive pattern were reported across the specie's spatial distribution. To determine a sustainable level of fishing mortality for spiny lobster, we need to derive information on key population parameters, particularly those concerning the reproductive biology of the species in the Taiwan coastal waters.

The objective of this study is to evaluate the reproductive biology and its dynamics of *P. penicillatus* in the southeastern coastal waters off Taiwan (i.e., Taitung). We determined the reproductive activity based on histological techniques and provided a detailed description of ovarian development. Key parameters required in stock assessment including sex ratio, reproductive season, size at maturity and brood size were also evaluated and estimated.

Materials and methods

Sample collection

Samples were randomly collected from the catch in trammel nets and skin diving fisheries, monthly in Taitung (Fig. 1) during September 2003 to December 2004. For each lobster the carapace length, from the tip of the rostral spine to the posterior edge, was measured to the nearest 0.01 mm. Sex, reproductive state, the presence of external eggs and spermatophore condition, were recorded on the day of collection. A total of eighteen 5 mm^3 small ovary samples from pair ovaries of three lobsters, were obtained from three sections (anterior, middle and posterior) of each ovary lobe. Oocytes from each section were measured using a computerized image analyzing system (Image Pro-Plus v. 5.0) linked to a microscope. Applying a split-plot ANOVA, we found that there were no significant differences in the size of oocytes between lobes in each ovary ($F_{1,24} = 0.54$, $P > 0.05$). This was expected as both ovary lobes were at the same stage of oocyte development. About 20 ovary samples were dissected every month from January 2004 to December 2004. Each ovary was weighted and fixed in Bouin's solution, sectioned at 7 μm and stained with Mayer's haematoxylin and Eosin. Egg masses were removed from berried females for fecundity estimation.

Gonad maturation and breeding period determination

The stage of ovary maturity was determined based on Minagawa and Sano (1997) and Junio (1987). According to the most advanced group of oocytes present in the sample, we classified the five stages of maturity as (1) immature stage, (2) developing/redeveloping stage, (3) ripe/re-ripe stage, (4) spent stage, (5) recovery stage. A gonadosomatic index (GSI) was determined for an individual female (Minagawa 1997) as

$$\mathrm{GSI} = \frac{W_\mathrm{g}}{CL^3} \times 10^5$$

where W_g represents the gonad weight (g), and CL is the carapace length.

The spawning time was determined by the following three methods: (1) the temporal development of the ovaries in females (Junio 1987; Chubb 2000), (2) the evolution of temporal changes in females' GSI (Junio 1987; Plaut 1993; Goñi et al. 2003), and (3) seasonal

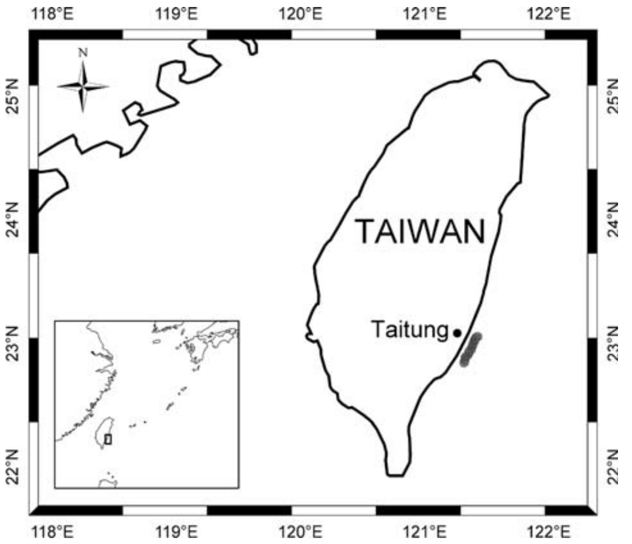

Fig. 1 Map of the study area showing the location (*spotted zone*) where the spiny lobster *Panulirus penicillatus* was sampled

changes in the composition of ovigerous females (Minagawa 1997).

Size at maturity

The size for physiological maturity is defined as the size at which ovaries are in developing stage or higher during reproductive season, and the size for functional maturity is defined as the size at which females are involved in the reproductive activity and berried (Evans et al. 1995).

For female lobsters, the size at which 50% of all individuals are physiologically and functionally mature (CL_{50}) was determined from modeling size-specific proportion of mature ovaries in each 5 mm CL class and external reproductively active individuals in each 3 mm CL class, respectively. A conventional logistic model (Minagawa 1997; Goñi et al. 2003) was used to quantify such a relationship:

$$P = \frac{1}{1 + \exp[r \times (CL - CL_{50})]}$$

where P is the proportion of mature individuals within a size class, r is the slope of the curve, and CL_{50} is the size (CL) at 50% sexual maturity, and CL is carapace length. CL_{50} and r were estimated using the nonlinear least square procedure (Chambers and Hastie 1992) implemented with the S-Plus (MathSoft Inc.).

For male lobsters, it is not possible to determine physiological maturity from external characteristics or the macroscopic appearance of the testes (Aiken and Waddy 1980; Chubb 2000). Thus, the functional maturity for males was based on the onset of allometric growth of the walking leg (George and Morgan 1979). It is difficult to make precise measurement of the whole walking leg, thus in present study measurements were made for the meropodite length (the longest segment of the limb) of the right walking leg (Evans et al. 1995). The initiation of allometric growth was determined by plotting the second and third meropodite length against the carapace length. The lowest combined residual sum of square for paired regressions indicated the point of onset of allometric growth, which is the size at maturity for males defined by Somerton (1980) and Lovett and Felder (1989). For females, the same method was attempted for estimating the size at maturity. After determination of the inflection point, the following F-statistics was calculated.

$$F = \frac{(RSS_1\text{line} - RSS_2\text{line})/2}{RSS_2\text{line}/(N - 4)}$$

where RSS_1line is the residual sum of square (RSS) of fitting a single regression model to the data, RSS_2line is the RSS of fitting two regression models to the data and N is the number of data points. This F-statistics was then compared with critical F value for determining if the resulting two regression models fit the data better than a single regression model (Somerton 1980). Analysis of covariance (ANCOVA) was used to evaluate whether the slopes of the regression lines were significantly different (Minagawa and Higuchi 1997).

Brood size

Brood size is defined as the number of eggs carried externally on the pleopods of once spawning (Pollock and Goosen 1991). Twelve egg masses in the early stage of development (Beyers and Goosen 1987) borne by females selected to cover a wide size range were collected for brood size estimates (Juinio 1987). Egg masses were cleaned of non-egg material and oven-dried at 80°C for 4–5 h (Gomez et al. 1994). The total dried weight was determined to the nearest 0.0001 g with an electronic balance. The mean number of eggs in three 0.01 g subsamples per egg batch was used to calculate brood size and relative brood size (i.e., egg per body gram, Hobday and Ryan 1997; Goñi et al. 2003).

Relative reproductive potential

The relative reproductive potential (RRP) was estimated for *P. penicillatus* as follows:

$$\text{RRP} = C_i \times M_i \times B_i$$

where C_i is the proportion of the size-class i in all females, M_i is the proportion of ovigerous females in size-class i, and B_i is the mean brood size of females in size-class i (Hobday and Ryan 1997; Goñi et al. 2003).

Results

Size distribution and sex ratio

From January 2003 to December 2004, a total of 2068 *P. penicillatus* were randomly sampled along the Taitung coast, of which 1,031 were male and 1,037 were female. Most males sampled had sizes ranging from 40 to 60 mm CL, females were from 40 to 65 mm CL and ovigerous from 45 to 80 mm CL (Fig. 2).

The sex ratio fluctuated from 0.4 to 0.6 without a systematic pattern at a CL of less than 80 mm, but the proportion of females decreased with CL when CL was greater than 80 mm. The sex ratios remained between 0.4 and 0.6, irrespective of the month. The overall sex ratio did not differ significantly from 0.5 during the sampling period ($\chi^2 = 0.02$, $P > 0.05$). However, more females occurred in the samples collected in June, July and September (mean = 0.58; SE = 0.006).

Oocyte and ovary development

The developmental stage of almost all oocytes in the anterior, middle and posterior areas of ovaries was isochronal, and the oocyte frequency distribution (Fig. 3) indicated an apparent mode moving with the ovarian development. This suggests that almost all the oocytes in an ovary are spawned at the same time. Based on microscopic characteristics, seven oogenesis stages were defined for the spiny lobster (Table 1, Fig. 4).

The gonads were collected from 157 females of size ranges from 43.60 to 90.34 mm CL. Based on the oocyte development, GSI and macroscopic examination by the naked eye, we developed a classification scheme for the ovary development of female lobster (Table 2). For females, ovaries classified as the developing or later stages in maturation were categorized as physiologically mature.

Reproductive activity

The GSI of females increased from 0.46 in April to the peak of 1.36 in May, decreased thereafter to the lowest value of 0.31 in October, and then gradually increased (Fig. 5).

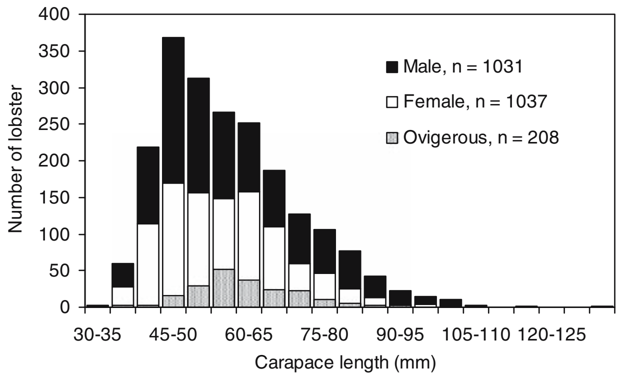

Fig. 2 Length-frequency distribution of the spiny lobster *Panulirus penicillatus* sampled in Taitung between September 2003 and December 2004

Egg-bearing females were observed from September 2003 to December 2003 and throughout 2004. A size-specific spawning time was observed by dividing carapace lengths into three classes (Fig. 6). The proportion of size combined ovigerous females were high from April to July, peaked in June (50%), and then deceased in August. The smallest size of ovigerous females found in this study was 43.53 mm CL.

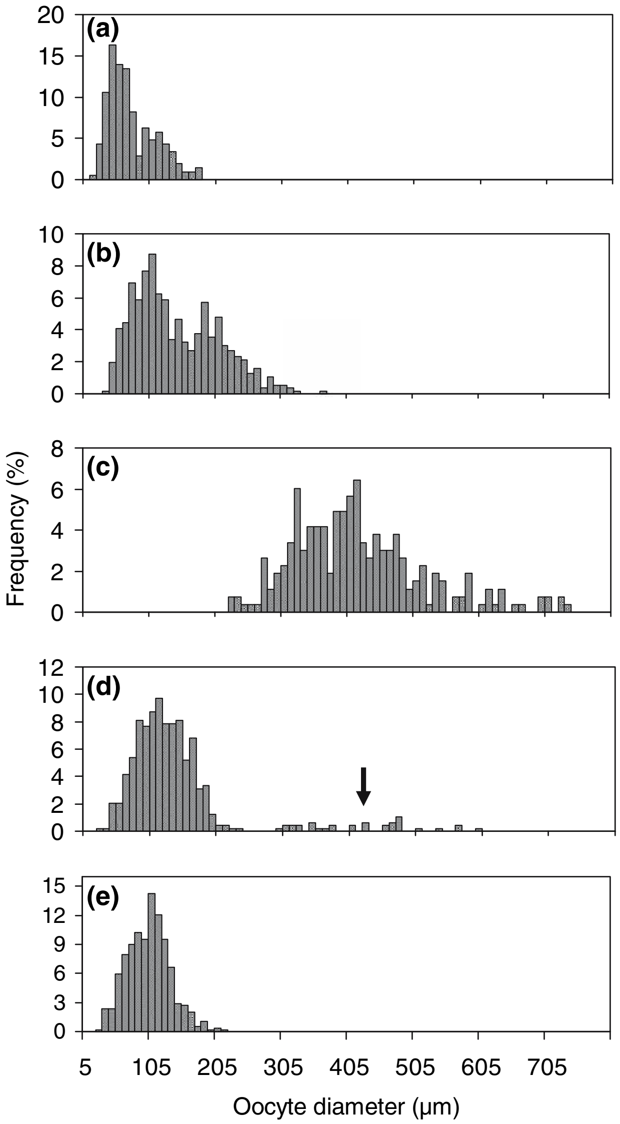

Fig. 3 Individual lobster oocyte diameter distribution at different stages of ovarian development obtained from histological section. **a** Inactive stage (52.51 mm CL) with most advanced group of oocytes (MAGO) in pre-yolk platelet stage, **b** developing stage (56.08 mm CL) with MAGO in yolk platelet stage, **c** ripe stage (66.56 mm CL) with MAGO in pre-mature and maturation stage, **d** spent stage (76.71 mm CL) with MAGO in maturation and yolk platelet stage, **e** recovery stage (63.37 mm CL) with MAGO in pre-yolk platelet stage. (*Arrow* indicates the residual oocytes)

Table 1 Stages of oogenesis and their microscopic characteristics in the spiny lobster *Panulirus penicillatus*

Oogenesis stage	Oocyte diameter (mean ± SE μm)	Nucleus diameter (mean ± SE μm)	Follicle cell (mean ± SE μm)
Multiplication			
Oogonium (I)	10.54 ± 0.35	7.46 ± 0.16	–
Pre-vitellogenesis			
Chromatin nucleolus (II)	18.51 ± 0.39	13.8 ± 0.93	–
Vitellogenesis			
Oil globule (III)	46.41 ± 1.59	17.99 ± 0.74	3.98 ± 0.43
Pre-yolk platelet (IV)	130.27 ± 3.17	36.31 ± 0.74	3.8 ± 0.14
Yolk platelet (V)	239.61 ± 5.44	48.65 ± 1.56	2.72 ± 0.21
Pre-mature (VI)	428.82 ± 12.40	47.33 ± 1.48	2.6 ± 0.12
Maturation			
Maturation (VII)	590.64 ± 25.65	–	2.52 ± 0.16

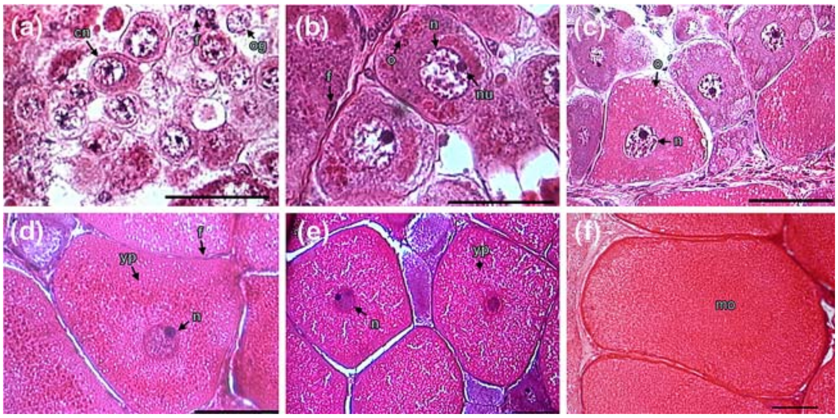

Fig. 4 Histological section illustrating oocytes at different maturity stages of the spiny lobster *Panulirus penicillatus*: **a** Oogonia and chromatin nucleolus stage, with a large central nucleus (Scale bar = 50 μm); **b** Oil globule stage, with one or two large oil globules appearing near the nucleolus; **c** Pre-yolk platelet stage, globules diffuse peripherally; **d** Yolk platelet stage, the nucleus diameter reaches its maximum; **e** Pre-mature stage, the nucleus becomes shrunk; **f** Maturation stage, the oocyte diameter reaches maximum and follicle cells are hardly visible. (Scale bar = 100 μm, *og* oogonia, *cn* oocyte at the chromatin nucleolus stage, *f* follicle cell, *o* oil globule, *n* nucleus, *nu* nucleolus, *yp* yolk platelet, *mo* mature oocyte)

Ovarian development corresponded well with the changes in GSI and ovigerous percentage (Fig. 7). The ovaries in developing stage were observed from February to November, and peaked in August (50%). Individuals with the ovaries in ripe stage appeared from January to March and May to December. Higher percentages were found in May through July, and peaked in June (36%). The presence of immature and recovery stage ovaries were observed year-round. The re-developing or re-ripe stage ovaries were found in March, and May to July

Size at 50% maturity

A total of 157 females with a size range from 43.60 to 90.34 mm CL were used to estimate size at physiological maturity. Changes in the proportion of physiologically mature females with size class (5 mm intervals) were described by the logistic curve for estimating the CL_{50} as:

$$P = \frac{1}{1 + \exp\left[-0.28 \times (CL - 56.46)\right]}$$

$r^2 = 0.983$ and $n = 157$. The mean and standard error for the CL at physiological maturity CL_{50} were 56.46 ± 0.56 mm CL (mean ± SE) (Fig. 8).

Carapace length at functional maturity was estimated based on the presence of berried eggs or spermatophore using the data collected in 2003–2004,

$$P = \frac{1}{1 + \exp\left[-0.11 \times (CL - 66.63)\right]}$$

Table 2 Classification and description of macroscopic and microscopic ovary stages of spiny lobster *Panulirus penicillatus*

Ovarian stage	Macroscopic appearance	Histological characteristics	GSI (mean ± SE)	*n*	Most advanced oocyte substage
Inactive	Ovaries were white rod-like, occupying a small part of the cephalothoracic cavity	Oocytes protrude from the germinal nest to the periphery of an ovary	0.22 ± 0.03	40	Pre-yolk platelet
Developing/re-developing	The ovary increased in size and turned light orange or orange as the ova developed	The ovarian wall was thin, more mature ova radiated towards the ovarian wall. Re-developing ovary had thicker ovarian wall than developing ovary and the oocytes were scattered	1.04 ± 0.12 1.13 ± 0.24[a]	25 7[a]	Yolk-platelet Yolk-platelet[a]
Ripe/re-ripe	The swollen dark orange ovaries occupied a large part of the cephalothoracic cavity	The pre-mature and mature oocytes were tightly packed together, thus distorted in shape. The re-ripe ovaries were similar to those in ripe stages	3.7 ± 0.37 2.37 ± 0.43[b]	21 7[b]	Pre-mature Maturation[b]
Spent	The ovaries were flaccid and white or light yellow in color. Some remaining mature oocytes could be observed by eyes	Un-spawned mature oocytes and some yolk platelet oocytes were undergoing re-sorption	0.66 ± 0.09	8	Maturation or yolk platelet (but atretic)
Recovery	Ovaries were thin and white, and the ovarian wall was thick	The most advanced oocytes were at the pre-yolk stage, but some of them underwent re-sorption	0.52 ± 0.03	44	Pre-yolk platelet (but atretic)

[a] Denotes the re-developing stage

[b] Denotes the re-ripe stage

$r^2 = 0.950$, $n = 1036$, and 3 mm was used as the interval of size class. The mean and standard error for the CL at functional maturity CL_{50} was 66.63 ± 1.07 mm CL (Fig. 8).

For males, the allometric growth of both the right second and third meropodite (RSM and RTM) was described by two regression lines (Fig. 9a, b). Inflection points occurred at 72.21 mm CL in RSM [slopes were 0.59 ± 0.01 (mean ± SE) and 1.03 ± 0.04, respectively] and 74.43 mm CL in RTM (slopes were 0.63 ± 0.01 and 1.04 ± 0.04, respectively). For females, we failed to find the allometric growth of RSM (slope was 0.53 ± 0.02) and RTM (0.53 ± 0.02) (Fig. 9a, b). An analysis of residual sum of square indicated that two regression lines fit better in RSM and RTM for males (F test, $P < 0.001$).

Regression lines were statistically compared with each other on sex, size, and between appendages by ANCOVA. For males, slopes were significantly different between immature and mature individuals in RSM ($F = 243.1$, $P < 0.01$) and RTM ($F = 194.7$, $P < 0.01$). Sex-specific growth of RSM ($F = 4.88$, $P < 0.05$) and RTM ($F = 11.43$, $P < 0.01$) was observed in this study, and the RSM grew larger than RTM for immature males ($F = 4.84$, $P < 0.05$).

Brood size

The brood size of spiny lobster was size related, and brood size increased progressively with body size

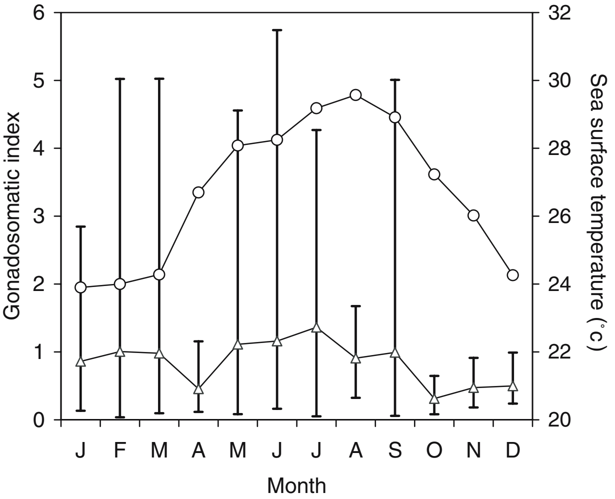

Fig. 5 Monthly variation in mean gonadosomatic index (GSI) of the female spiny lobster *Panulirus penicillatus* in Taitung (*open triangle* = average, *vertical bars* = ranges), and the mean sea surface temperature off the Taitung coast (*open circle*) between January 2004 and December 2004

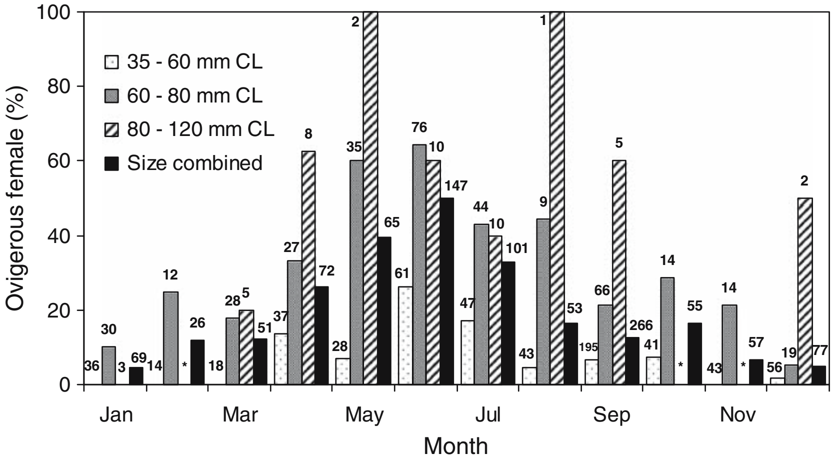

Fig. 6 Monthly presence of egg-bearing *Panulirus penicillatus* by size class pooled from September 2003 to December 2004. Number of bars show the number of individuals. *Asterisks* denote no data

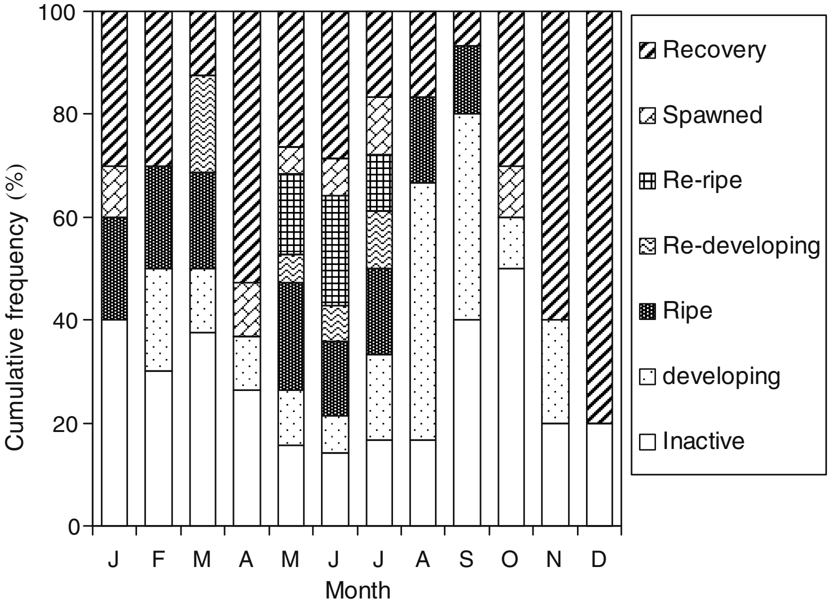

Fig. 7 Cumulative frequencies (%) of individuals by month for each stage of ovarian development of the spiny lobster *Panulirus penicillatus* in Taitung

(Fig. 10). The relationship between CL and the number of oviposited eggs (Y_{BS}) over a size range of 44.51 to 80.54 mm CL was estimated as:

$$Y_{BS} = 2.4 \times 10^{-3} CL^{4.18}$$

($r^2 = 0.902$, and $n = 12$)

The total dried egg masses ranged from 0.63 to 6.66 g. The mean number of eggs per 0.01 g subsample ranged from 253 to 265 eggs. The estimated total number of eggs over the sampled size range was from 16,399 to 173,090 eggs, and the mean egg size range was from 524 to 610 μm in diameter. The number of eggs per body gram ranged from 204 to 537 eggs, and there were no significant relationships between the relative brood size and body size ($r = 0.56$, $P > 0.05$) and between the egg size and brood size ($r = 0.1$, $P > 0.05$).

Relative reproductive potential

The lobsters in the size class of 60–80 mm CL yielded 62.4% of the total egg production, highest among all size classes (Fig. 11). Lobsters smaller than 60 mm CL contained more than 50% of the total commercial catch, but produced only 7.93% of the eggs. Lobsters in size class 95–100 mm CL had the highest productivity ratio ($P_i = E_i\%/C_i$) 20.35%, which made the lobsters in this size class were 2.7 times more productive than the lobsters in the 60–80 mm CL.

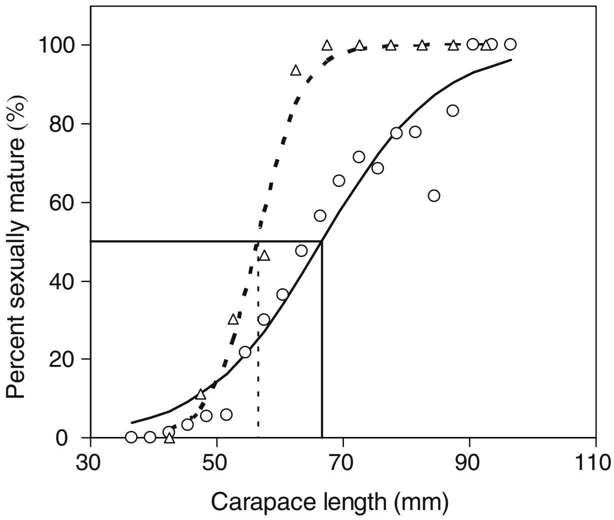

Fig. 8 Scatter plots and fitted curves for the relationship between body size (carapace length) and percent sexual maturity based on functional maturity gauged by presence–absence of sperm mass or berried condition (*dark-line curve*), and based on physiological maturity by microscopic examination of ovaries (*dotted curve*), and analogous perpendicular lines are median size (CL_{50}) at functional and physiological maturity, respectively

Discussion and conclusions

Sex ratio

The sex ratio of *P. penicillatus* was 1:1 in the present study, which differed from observations made in other studies. The sex ratio was biased towards males of *P. penicillatus* population in Hawaiian (McGinnis 1972), and in Red Sea (Hogarth and Barratt 1996). In contrast, the sex ratio of *P. penicillatus* favored females over males in Marshall Islands (0.71) (Ebert and Ford 1986), and in Gulf of Eilat (0.61) (Plaut and Fishelson 1991). The skewed sex ratio in theses studies might result from limited habitat coverage and use of single fishing gear over a relatively short time period in these studies because female and male lobsters tended to favor different habitats and have different susceptibility to different fishing gears (Hogarth and Barratt 1996; Ebert and Ford 1986). The samples of this study were collected with skin diving and trammel net and covered different habitats over a relatively long time period. Thus, the sex ratio tended to be more balanced and might reflect the true sex ratio of the *P. penicillatus* population in Taitung. Males dominated large size classes in the present study, which might result from sex-specific growth rate (Morgan 1980) or the reproductive cost of females (Briones-Fourzán and Lozano-Alvarez 1992).

Females were more abundant than males in June, July and September 2004, which were the reproductive

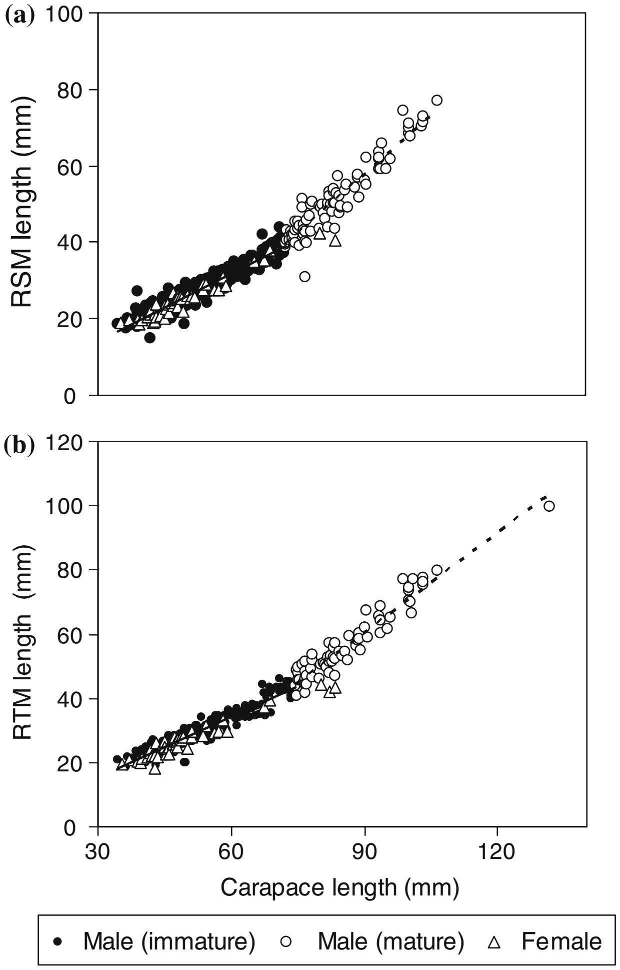

Fig. 9 Scatter plots of the relationship between **a** right second meropodite (RSM) length and **b** right third meropodite (RTM) length and carapace length for the spiny lobster *Panulirus penicillatus*

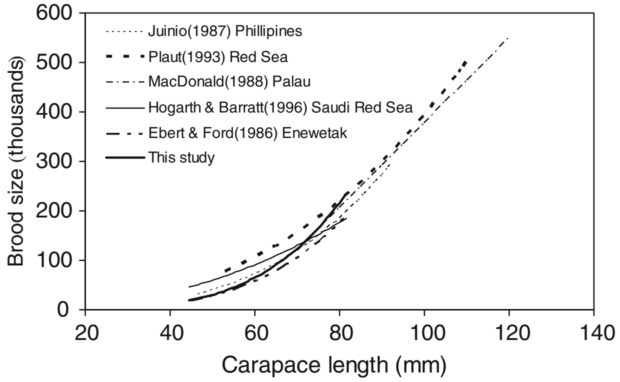

Fig. 10 Comparison of the relationships between carapace length and brood size of *Panulirus penicillatus* among various studies

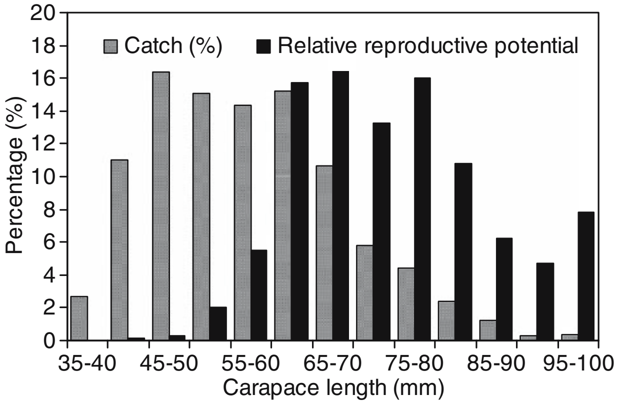

Fig. 11 Relative reproductive potential and the corresponding percentage of the commercial catch in Taitung, by 5-mm size class

season. This result tends to be contrary to the spawning behavior of female lobsters that usually display a more reclusive behavior and tend to occupy the deepest parts of the habitat during the spawning season (Kanciruk and Herrnkind 1976; Morgan 1980).

Size at maturity

For females, the estimate of size at 50% functional maturity was 66.63 mm CL, and the size at 50% physiological maturity was 56.46 mm CL. Size at maturity of *P. penicillatus* was found to have large spatial variations (Table 3). In the estimation of size at functional maturity, a necessary prerequisite is to accurately identify the maturation state. A histological analysis of the developmental stages of oocytes is the most accurate method for determining sexual maturity, because unberried but mature females are indistinguishable from external morphology (DeMartini et al. 2005). In addition, the sample size and sampling time and season covered by a study can also influence the result.

In this study, we found that mean GSI value can be used to distinguish different ovaries stages, although GSI can be influenced by a number of factors such as variations in weight-length relationships among individuals. The result was similar to that reported for *P. japonicus* by Minagawa and Sano (1997).

The difference in size at maturity can also result from biotic and abiotic environmental variables such as population density (Pollock 1995; DeMartini et al. 2003), temperature (Chittleborough 1976), food availability (Kanciruk 1980), and shelter (Polovina 1989). If we consider size at maturity is related to age (Fielder 1964), we may infer that the growth of *P. penicillatus* in Taitung is faster than that of lobsters in the other study sites. For males, the allometric growth of the walking leg after a pubertal molt provides useful estimates of size at functional maturity in male lobsters for *P. versicolor* (George and Morgan 1979), *P. japonicus* (Minagawa and Higuchi 1997), and *P. guttatus* (Robertson and Butler 2003).

The size at maturity for male *P. penicillatus* was calculated as 72.21 mm CL and 74.43 mm CL by RSM and RTM, respectively. This suggests that the RSM and RTM provide approximate estimates and can be useful for determining the functional maturity for males. A similar size at maturity of 70 mm CL was determined by the allometric growth of the third

Table 3 A comparison of the estimated size at sexual maturity of the spiny lobster *Panulirus penicillatus* among various studies. SAM is the size at maturity (in mm CL)

Area	Author	Method	SAM
Oahu, Hawaii	MacDonald (1979)	Based on the average CL of berried female	98
Palau	MacDonald (1979)	Based on the average CL of berried female	100
Enewetak Atoll, Marshall Islands	Ebert and Ford 1986	Based on the smallest berried female	62
Cagayan, Philippines	Junio (1987)	Based on the average CL of mated or berried female	45–49.9
Western Caroline Islands, Palau	MacDonald (1988)	Based on the smallest berried female	69
Gulf of Eilat, Red Sea	Plaut (1993)	Incidence of mated or berried females Relationship between CL and the Pleopodal exopodite length	50
Saudi Red Sea	Hogarth and Barratt 1996	Incidence of mated or berried females Relationship between CL and the 2nd or 3rd pereiopod Smallest berried female	40–50
Taitung coast, Taiwan	This study	Incidence of mated or berried females Histological analysis	66.63[a] 56.46[b]

[a] Denotes size at 50% functional maturity

[b] Denotes size at 50% physiological maturity

walking leg length in Juinio (1987). For females, RSM or RTM fails to produce a morphological index to discriminate between mature and immature lobsters, as in the study of Plaut (1993) by first and fifth limb length and in *P. versicolor* (George and Morgan 1979).

Reproductive cycle

The major spawning season of *P. penicillatus* in Taitung is from May to September, based on the monthly pattern of ovarian development, the percentage of ovigerous females and GSI. *P. penicillatus* in the northern hemisphere were reported to spawn actively throughout a year, with high spawning season during summer (Morris 1968; MacDonald 1979, 1988; Ebert and Ford 1986; Juinio 1987; Plaut 1993). This high breeding activity in summer results from higher temperature (Fig. 5; Plaut 1993). In this study, the appearance of re-developing and re-ripe stage ovary from May to July suggests that females recover quickly for repeating spawning results from higher temperature (Figs. 5, 7).

An examination of monthly presence of egg-bearing by size class of *P. penicillatus* indicates that spawning season may be size-specific (Fig. 6). Large females (>60 mm CL) tend to spawn early in spring, whereas smaller females (<60 mm CL) spawn in summer. It is difficult to numerate how many time lobsters of a given size class spawn in a year (Juinio 1987; Plaut 1993).

The lobsters of size greater than 60 mm CL observed have more re-developing and re-ripe ovaries than smaller lobsters (< 60 mm CL; Fig. 12), and the smallest re-developing female identified in this study was 57 mm CL. This suggests that large mature females (>60 mm CL) spawn at least three times a year while smaller newly mature females spawn at least once. For other *P. penicillatus* populations, mature females are estimated to spawn 2–4 times in Red Sea and up to four times a year in Philippines (Plaut 1993; Juinio 1987). The tropical *Panulirus* species may spawn year round when they are not molting (Chubb 2000).

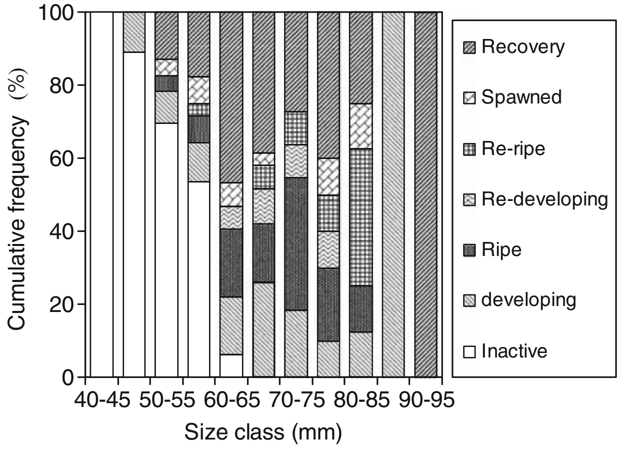

Fig. 12 Cumulative frequencies (%) of individuals by size class (5-mm carapace length) for each stage of ovarian development of the spiny lobster *Panulirus penicillatus* from Taitung, Taiwan

Brood size

The relationship between CL and brood size in *P. penicillatus* from Taitung was curvilinear, as found in the Philippines (Juinio 1987) and the Red Sea (Plaut 1993; Hogarth and Barratt 1996), but MacDonald (1988) showed a linear relationship in Palau. The difference may result from different size ranges of samples. In general, lobsters with the same CL tend to yield similar numbers of eggs regardless of the relationship (Chubb 2000). Spatial variations in CL-brood size relationships were reported in certain subtropical and temperate lobsters (Chubb 2000). Although the sample size of this study is not large, the relationship between CL and brood size in females of *P. penicillatus* in Taitung is consistent with that for other populations (MacDonald 1979; Juinio 1987; Plaut 1993; Hogarth and Barratt 1996; Fig. 10). This confirms the result of Plaut (1993) who suggests that the relationship between CL and brood size is constant in *P. penicillatus* over a wide range of environment conditions.

Many lobster species have reduction in brood size for repeat spawning within the same season (Chubb 2000). Previous studies did not evaluate variations in repetitive brood sizes of *P. penicillatus* (Juinio 1987; Plaut 1993). By comparing GSI of the developing and ripe stage ovaries with the re-developing and re-ripe stage ovaries, we found that the number of eggs in the second spawning event in a given year tended to be smaller than that in the first spawning.

Reproductive senescence was noted in the large females of some spiny lobsters (Chubb 2000). Goñi et al. (2003) showed that maximum relative brood size occurred in the median size class of the *P. elephas* population in the mediterranean, and the egg size tended to increase with body size. The relative brood size and egg size were not significantly related to the body size and brood size of *P. penicillatus* in Taitung. This is similar to what was observed for the *P. penicillatus* in Philippines (Juinio 1987).

Relative reproductive potential

Relative reproductive potential can serve to determine the size class of spawning females that make the greatest contribution to the egg production in a population (Kanciruk and Herrnkind 1976). Female lobsters of 60–80 mm CL make the greatest contributions to egg production, and more than 50% of the females in commercial catch had their sizes smaller than or equal to 60 mm CL in Taitung (Fig. 11). This indicated that the smaller lobsters (≤60 mm CL) contributed lower egg production (7.93 %), but consisted of a large part of the commercial catch.

The minimum legal size (MLS) should be established at a size that allows each individual an opportunity to reproduce at least once before reaching the exploitable size (Jamieson 1993). In the present study, the size at 50% physiological maturity of females was 56.46 mm CL (about 3 years old, Chen 2005). Current MLS protects 54.36% of egg production potential, and thus tends to be effective in conserving egg production. However, this MLS is 16.61 mm larger than the size at maturity, which may be overcautious in the long term.

An implementation of a MLS of 65 mm CL would have less impact on the overall egg production because of low RRP of lobsters in these size classes. However, such a regulation may be necessary. It can allow lobsters to reproduce at least once before reaching the harvestable size and protect 23.68% of population egg production.

The lobsters that have the re-developing and re-ripe stages of ovary had an average size of 70.4 mm CL, and the lobsters in size class 95–100 mm CL had the highest productivity ratio (20.35%). Thus, large females are important for the egg production because they are highly fecund, produce large and high quality of eggs and are capable of spawning multiple times annually.

Introducing a maximum legal size (MALS) of 90 mm CL can protect 12.59% population egg production capacity, even though only 0.68% of the catch falls in this size (≥90 mm CL). This strategy, however, may have side effects because it may lead to an increased exploitation of the remaining legal-size females (Hobday and Ryan 1997). However, given the small number of catch in this size range, this possible side effect may not be significant for the Taitung lobster fishery. If the implementation of MLS (65 mm CL) and the MALS (90 mm CL) can be introduced at the same time, we would protect 36.27% of the total egg production.

Conclusions

The spiny lobsters, *P. penicillatus*, had an extended spawning time period throughout a year in Taitung, although spawning was most intense between May and September. The presence of highly reproductive females and repetitive spawning during the summer spawning season in Taitung coastal water were linked to higher water temperature. Spatial variations of size at maturity were found in *P. penicillatus*. For females the size at 50% physiological maturity was 56.46 mm CL, size at 50% functional maturity was 66.63 mm CL and for males size at functional maturity was between 72 and 74 mm CL. There was a curvilinear relationship between brood size and carapace length, with an average of 0.1 million eggs in females ranging in size from 44.51 to 80.54 mm CL. If we implemented the MLS (65 mm CL) and MALS (90 mm CL) at the same time, it would increase the egg production potential of the population. The study of relative reproductive potential provides us with the critical information needed for the establishment of size limit regulation. However, a better understanding of the lobster population dynamics requires a better understanding of key life history processes such as growth, mortality, and larval dispersal mechanism of *P. penicillatus*. An establishment of a realistic population dynamics model that mimics the lobster life history and the fishery process should be the focus of future research for the lobster population in Taitung.

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